

AD-A049 853

WISCONSIN UNIV MADISON DEPT OF VETERINARY SCIENCE
ECOLOGICAL AND AEROSPACE MEDICAL ASPECTS OF VIRUS DISEASES. PAR--ETC(U)
OCT 74 R P HANSON, T M YUILL

F/G 6/3

AFOSR-72-2337

AFOSR-TR-75-1645-REV

NL

UNCLASSIFIED

194

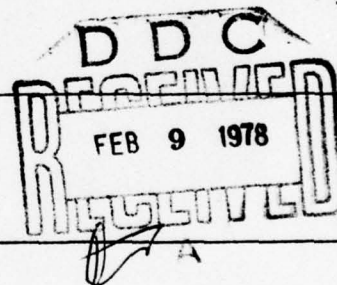
ADA049 853



REPORT DOCUMENTATION PAGE

READ INSTRUCTIONS
BEFORE COMPLETING FORM

1. REPORT NUMBER AFOSR-75-1645	2. GOVT ACCESSION NO.	3. RECIPIENT'S CATALOG NUMBER
4. TITLE (and Subtitle) Biological and Aerospace Medical Aspects of Virus Diseases PART II. ENTOMOLOGICAL STUDIES. Revised.		5. TYPE OF REPORT & PERIOD COVERED Final Report.
6. AUTHOR(s) Robert P. Hanson Thomas M. Yuill		7. PERFORMING ORG. REPORT NUMBER AFOSR-72-2337
8. AUTHORING OR GRANT NUMBER(s)		9. PROGRAM ELEMENT, PROJECT, TASK AREA & WORK UNIT NUMBERS 61102F19777 681512
10. PERFORMING ORGANIZATION NAME AND ADDRESS University of Wisconsin Department of Veterinary Science Madison, Wisconsin 53706		11. REPORT DATE Oct 74
12. CONTROLLING OFFICE NAME AND ADDRESS Air Force Office of Scientific Research (NL) Bolling AFB DC 20332		13. NUMBER OF PAGES 308 (12353p.)
14. MONITORING AGENCY NAME & ADDRESS (if different from Controlling Office) AFOSR		15. SECURITY CLASS. (of this report) Unclassified
16. DISTRIBUTION STATEMENT (of this Report) Approved for public release; distribution unlimited.		17. DISTRIBUTION STATEMENT (of the abstract entered in Block 20, if different from Report)
18. SUPPLEMENTARY NOTES Supersedes A019543		19. KEY WORDS (Continue on reverse side if necessary and identify by block number) These
20. ABSTRACT (Continue on reverse side if necessary and identify by block number) The entomological studies reported in this volume represent an effort to document environmental changes, such as habitat availability, host availability and climate, as they relate to the abundance and distribution of hematophagous Diptera. Some studies were conducted in primary and secondary forests and associated clearings which are areas of early ecological disturbance. Other studies were performed in an area of great ecological disturbance. The data show that the ecological changes have altered		



DD FORM 1 JAN 73 1473

EDITION OF 1 NOV 65 IS OBSOLETE

UNCLASSIFIED

SECURITY CLASSIFICATION OF THIS PAGE (When Data Entered)

406801

20. ABSTRACT - Contd.

populations of biting insects and influence the potential and actual risk of transmission of arthropod-borne pathogens of man and domesticated animals.

Topics covered include: → (cont on p. iii)

ii

UNCLASSIFIED

SECURITY CLASSIFICATION OF THIS PAGE(When Data Entered)

AFOSR-TR-75-1645

*Ecological and Aerospace Medical Aspects
of Virus Diseases.* PART II

Entomological Studies

REVISION for	
NTIS	White Section <input checked="" type="checkbox"/>
DDC	Diff. Section <input type="checkbox"/>
UNANNOUNCED	<input type="checkbox"/>
JUSTIFICATION	
DISTRIBUTION/AVAILABILITY CODER	
Dist.	Avail. and/or SPECIAL
A	

Introduction

II-1

Abstracts

II-2

The Man-Biting Activity of Haematophagous Diptera in a
Neotropical Rain Forest Environment

Introduction

II-9

Study Areas

II-15

Materials and Methods

II-40

Phlebotominae

II-64

Ceratopogonidae

II-241

Tabanidae

II-258

Simuliidae, and

II-274

Culicidae, and

II-286

Mosquito Studies in a Lowland Cattle Producing Region,

II-313

AIR FORCE OFFICE OF SCIENTIFIC RESEARCH (AFSC)
NOTICE OF TRANSMITTAL TO DDC
This technical report has been reviewed and is
approved for public release in accordance with AFR 190-12 (7b).
Distribution is unlimited.
A. D. BLOSE
Technical Information Officer

Approved for public release;
distribution unlimited.

INTRODUCTION

The presence of insect-borne pathogens of vertebrates and the frequency of transmission will depend on the relative abundance of vector populations, the presence of suitable numbers of their vertebrate hosts and the habits and longevity of the arthropods themselves. Habitat availability, host availability and climate, then, are all key factors in the transmission of these pathogens. The rapid changes being made in tropical forests, and their conversion to open areas for crop and pasture, dramatically alter these factors.

The entomological studies represent an effort to document some of these changes as they relate to the abundance and distribution of hematophagous Diptera. The Providencia studies were conducted in primary and secondary forests and associated clearings. This was an area of early ecological disturbance. The Caucasia area is one of great disturbance. The original forest is nearly gone, having been replaced by extensive pastures. These changes have altered populations of biting insects, and influence the potential and actual risk of transmission of arthropod-borne pathogens of man and his domesticated animals.

THE MAN-BITING ACTIVITY OF HAEMATOPHAGOUS DIPTERA IN A
NEOTROPICAL RAIN FOREST ENVIRONMENT.

ABSTRACT: The entomological studies in the Providencia area were designed to obtain an overall view of man-biting activity by haematophagous Diptera in a rain forest environment. A series of biting catches of approximately 10 hours duration during the day and approximately 13 hours duration during the late evening and night were conducted at three forest sites and in a clearing adjacent to one of the forest sites. A considerable amount of information about the man-biting activity of the Phlebotominae, Culicoides, Simuliidae, Tabanidae, and Culicidae was obtained especially in relation to nocturnal and diurnal periodicity, seasonal fluctuations in population levels, habitat preferences, and vertical distribution.

Although subject to seasonal variation, human biting activity by haematophagous Diptera was most intense within the forest at night and can be primarily attributed to several species of Lutzomyia, of which L. hartmanni was the dominant, and Culicoides pseudodiabolicus, the most abundant man-biting species within the forest. In clearings biting activity by anthropophilic flies was greatest during the day due to relatively large numbers of black flies, especially Simulium metallicum. However, simuliids were often infrequent in the forests while mosquitoes, especially the arboreal Haemagogus capricorni falco, and in the summer tabanids, particularly Dichelacera chocoensis, dominated the biting activity.

Many interesting patterns of habitat and host utilization were elucidated.

In the forest series of catches, the predominant man-biting species and their percentage of the catch were Lutzomyia hartmanni (56%), L. trapidoi (22%), and L. yuilli (13%). In the clearing series of catches the predominant species were L. Hartmanni (56%), L. gomezi (16%), L. Yuilli (9%), and Warileya rotundipennis (9%).

For most species, both the magnitude and vertical stratification of their man-biting activity tended to be quite variable between the three forest sites. These differences were thought to be related to local variations in forest structure. Between-site differences in the magnitudes of biting activity were least pronounced in the understory. L. trapidoi, and to a lesser extent L. yuilli, were reluctant to bite at ground level in either the forest or clearing habitats. Their diminished biting activity at ground level appeared to primarily account for the greater similarity of the clearing catches to the forest floor catches than to those in the understory and canopy. In the clearing series of catches, the biting activity of L. hartmanni, L. trapidoi, and L. yuilli was detected to be significantly greater at the two forest edge sites than at those sites within the clearing. Diversity of man-biting activity in the clearing habitat was determined to be greatest at a site situated at the edge of pioneer vegetation and pasture. The pioneer vegetation extended to this location from the forest about 130 m away.

The man-biting activity of phlebotomine sandflies in the Providencia study area was primarily nocturnal although crepuscular patterns were exhibited by L. bifoliata within the forest and by L. gomezi at the clearing sites. The temporal pattern of biting activity of each of the predominant forest species, i.e., L. hartmanni, L. trapidoi, and L. yuilli, was quite variable from one night to another and there was often a sharp peak in the biting activity. When such variations were averaged, the emerged pattern.

MOSQUITO STUDIES IN A LOWLAND CATTLE PRODUCING REGION.

ABSTRACT: The Caucasia entomological studies concentrated on the collection of mosquitoes as they were quite abundant in this region. Most of the 51,683 specimens taken during the 14 months of the field studies were caught by means of CDC light traps and aspirator collections using a human as bait. The Caucasia region has a low but hilly topography. This area was once covered with forest but clearing for cattle production has been so extensive that only small scattered remnants remain.

The light trap collections were dominated by the Culex, especially by species in the subgenus Melanoconion, and by Anopheles triannulatus. Mansonia nigricans, M. titillans, and Aedeomyia squamipennis were also abundant in the light trap collections. The predominant man-biting species of this region include Aedes crinifer, A. scapularis, A. serratus and Psorophora albipes. Collections were made in forest, brushy, and pasture habitats at five different haciendas. Those species favoring the forest habitat include Aedes scapularis, Psorophora albipes, P. ferox and two species of Culex. Aedeomyia squamipennis, Wyeomyia species and a Culex species tended to be most abundant in the brushy areas. In open areas the predominant species included Anopheles triannulatus, Aedes crinifer, a Culex Melanoconion species, Mansonia nigricans, M. titillans, Psorophora cingulata and P. confinnis. Both light trap and aspirator catches were high during the rainy period from March through October but declined to low values during the November through March dry season. Psorophora albipes and Mansonia titillans accounted for 47% and 29% of the catch in a burrow-baited stable trap which was placed in a forested area on the Hacienda Barro.

THE MAN-BITING ACTIVITY OF HAEMATOPHAGOUS DIPTERA IN A
NEOTROPICAL RAIN FOREST ENVIRONMENT.

Charles H. Porter

TABLE OF CONTENTS

	Page
INTRODUCTION.	1
Previous Studies of the Phlebotomine Sandflies of Colombia	6
The Study Area and Its Climate.	8
Classification and General Description of the Forests in the Providencia Region.	17
Forest Platform Sites	20
Clearing Sites.	27
MATERIALS AND METHODS	33
Collecting Methods and Number of Catches.	33
Species Identification.	38
Data Analysis	41
RESULTS	57
Summary of the Common Species Taken in the Forest and Clearing Catches	57
Vertical Stratification of Man-biting Activity within the Forest.	59
Variation in Man-biting Activity between the Forest Sites.	73
Variation in Man-biting Activity between the Clearing Sites.	82

Differentiation of Microenvironments and Species on the Basis of the Man-biting Catches.	91
Summarization of the Temporal Patterns of Man-biting Activity in the Forest and Clearing Habitats	101
Seasonality of Man-biting Activity. . .	128
Species Using the Base of Trees as a Diurnal Resting Site.	133
DISCUSSION.	136
Definition of Terms	136
Comparison of Faunas.	137
Man-biting Activity in the Forests: Vertical Stratification and Between- site Differences.	141
Man-biting Activity in the Clearing . .	149
Variations in the Species Composition of the Anthropophilic Component between Different Microenvironments .	155
Selection of Microenvironment	161
Diel Periodicity of Man-biting Activity.	162
Seasonal Variations in Man-biting Activity.	170
Derivation of Interspecific Differ- ences in Biting Activity.	172
Species Using the Base of Trees as a Diurnal Resting Site.	174
The Common Man-biting Species of the Providencia Study Area.	175
<u>Lutzomyia bifoliata</u> Osorno-Mesa, Morales-Alarcón, de Osorno, and Muñoz de Hoyos, 1970.	175

<u>L. gomezi</u> (Nitzulescu), 1931. . . .	176
<u>L. hartmanni</u> (Fairchild and Hertig), 1957.	181
<u>L. panamensis</u> (Shannon), 1926 . . .	184
<u>L. tintinnabula</u> Christensen and Fairchild, 1971	191
<u>L. trapedoi</u> (Fairchild and Hertig), 1952.	192
<u>L. yuilli</u> Young and Porter, 1972. .	196
<u>Warileya rotundipennis</u> Fairchild and Hertig, 1951.	199
SUMMARY	201
BIBLIOGRAPHY.	206
APPENDICES	
A. Additional Historical Information about the Providencia Region	217
B. Additional Characteristics of the Forest Vegetation	219
C. Checklist of Phlebotomine Sandflies of the Providencia Region	230
D. The 132 Catches Used in the Ordination Analyses	232

THE MAN-BITING ACTIVITY OF HAEMATOPHAGOUS DIPTERA IN A
NEOTROPICAL RAIN FOREST ENVIRONMENT.

Charles H. Porter

An attempt was made to obtain an inclusive view of man-biting activity by all of the haematophagous Diptera within a Tropical Wet Forest environment; i.e., within both the forest and the adjacent clearing habitat. Previous investigations concerning the man-biting activity of Diptera in the Neotropics have, for the most part, evolved around the study of a particular disease and thus have tended to focus on the family involved in its transmission, e.g., yellow fever - Culicidae (Galindo et al. 1950 and many others), leishmaniasis - Phlebotominae (Williams 1970b, Disney 1968 and many others) and onchocerciasis - Simuliidae (Dalmat 1955). Faced with a number of complex systematic and statistical problems and finite support, I limited the present study to the phlebotomine sandflies. Our investigations of the other families will be completed as time and support permit.

A number of species of phlebotomine sandflies are known or suspected vectors of dermal (cutaneous and mucocutaneous) and visceral leishmaniasis in both the Old and

New Worlds (Lewis 1974). In the Neotropics dermal leishmaniasis appears to be endemic to many of the humid lowland forests (including the one in which the present study was made) where it occurs primarily as a zoonosis. In 1968, World Health Statistics Report indicated that from 1951 to 1965 there were 3,534 recorded cases of unspecified leishmaniasis in Colombia. Also, a number of arboviruses have been isolated from phlebotomine sandflies in Panama (Tesh et al. 1974) and Colombia (Barreto 1969). In spite of their importance in disease transmission, very little information exists concerning the man-biting activity of Phlebotominae in Colombia. The most extensive observations appear to be those included in the primarily taxonomic work of Young (1971).

The objective in this study was to determine the temporal and spatial attributes of the man-biting activity of phlebotomine sandflies in a Tropical Wet Forest environment. The daily periodicity (temporal pattern) of the man-biting activity of each of the common anthropophilic species was investigated. Comparisons were made between three forest sites of the magnitudes of biting activity and patterns of vertical stratification of the predominant man-biting species. In addition, the forest series of catches provided some information about seasonal fluctuations in biting activity. Comparisons of man-biting activity were also made between six clearing sites for several species.

The forest and clearing catches were differentiated as were the catches for the diverse microenvironments sampled within both of these habitats. The species using the base of large trees as a diurnal resting site were also noted.

For several groups of haematophagous Diptera including the phlebotomine sandflies, attempts have been made to divide the Neotropical biogeographical region into areas of endemism or dispersion (Lane 1953, Forattini 1957, Bram 1967, and Martins and Morales-Farias 1972). These authors indicate that the region of the present study lies in an area of faunal transition. I thus compared both the entire sandfly fauna and the anthropophilic component of the Providencia study area with those reported in the literature from neighboring regions.

A brief review of the biology of phlebotomine sandflies is included at this point for the benefit of those readers who are unfamiliar with these insects. Phlebotomine sandflies are most abundant in the humid tropics and subtropics but some species exist in arid habitats and temperate climates. A vast majority of the Neotropical species are sylvan. Their biology has been succinctly summarized by Tesh and Chaniotis (1975) as follows (references deleted):

Their life cycle consists of egg, four larval instars, pupa, and adult. The entire life cycle takes from 5 to 10 weeks, depending on species and the ambient temperature. The larvae develop in soil in warm, moist, shaded microhabitats protected from direct sunlight and rainfall, such as tree buttresses, animal burrows, caves, and crev-

ices in rocks and masonry. The larvae feed on decomposing organic matter, including dead insects, animal feces, leaf litter, and other rotting vegetation. Both immature stages and adults are very susceptible to dessication and require high humidity and constant moisture to survive. During periods of adverse climate, such as prolonged dry periods or cold, some species diapause as fourth instar larvae. . . . Most sandfly species are crepuscular and nocturnal in their biting activity.

Sandflies commonly move in short hops and rarely travel more than a few hundred meters from their resting and breeding sites. . . . The lifetime of sandflies under natural conditions is not precisely known, but laboratory data suggest that it is relatively short (2-5 weeks). Because each gonadotrophic cycle lasts 4-7 days . . .

An additional aspect of sandfly biology is the requirement by both sexes of a carbohydrate meal. Chaniotis (1975) found sugar-feeding to be a prerequisite for the initiation of blood-feeding in laboratory reared individuals of Lutzomyia trapidoi. He also observed that wild-caught females of this same species laid an average of 24.2 eggs. Autogeny has been noted in only a few species (Lewis 1971). The diurnal resting sites of Neotropical species include tree trunks, leaf litter, shrubs and saplings, animal burrows and tree hollows (Chaniotis et al. 1972). Comprehensive reviews of phlebotomine sandfly biology from a world-wide perspective have been written by Lewis (1971, 1974).

Previous Studies of the Phlebotomine
Sandflies of Colombia

Previous studies of the phlebotomine sandflies of Colombia have been primarily descriptive and have been comprehensively reviewed by Osorno-Mesa et al. (1967) and Barreto (1969). In 1972 Osorno-Mesa et al. summarized and updated the literature on the Colombian Phlebotominae. Osorno-Mesa et al. (1967) provided a list of the 23 species identified from Colombia to that date, indicated their geographic distribution, and described a new species. Barreto (1969) reported the presence of 14 additional species which were collected from the Pacific lowlands near Buenaventura. Young (1971) listed 69 species from Colombia and provided a key to their identification along with detailed illustrations of most species. Seventy-six species were recorded from Colombia by Osorno-Mesa et al. (1972a). They also presented their records of the geographic distribution of these species. Recently, additional new species from Colombia have been described by Young (1973), Young and Porter (1974), and Morales-Alarcón et al. (1974).

There is little information prior to the late 1960's concerning the specific identity of the man-biting phlebotomine sandflies of Colombia. Osorno-Mesa et al. (1967) observed what they considered at the time to be L. verrucarum (Townsend) biting man during both the day and night in the Department of Cundinamarca near the Río Bogotá at an altitude

of 2,550 m. Osorno et al. (1972b) showed that this was actually a new species which they named L. andina. From a series of collections made in the Pacific lowlands near Buenaventura in which humans were used as a bait, Barreto (1969) observed that the following species bit man: L. flaviscutellata (Mangabeira), L. hartmanni (Fairchild and Hertig), L. panamensis (Shannon), L. paraensis (Costa Lima), L. trapidoi (Fairchild and Hertig), and L. ylephiletor (Fairchild and Hertig). A series of man-biting catches were made at four sites in the Department of Choco by Young (1971) as part of a general survey of the phlebotomine sandfly fauna of the region. These catches were made between March and December of 1967 and apparently provide the only quantitative information about the man-biting activity of Phlebotominae in Colombia. The results of these catches are summarized in the discussion. Young and Porter (1972) reported L. yuilli to be a common man-biting species at the site of the present study. Several additional species were reported by Osorno-Mesa et al. (1972a) to be attracted to human bait in Colombia and include the anthropophilic L. lichyi (Floch and Abonnenc), L. longipalpis (Lutz and Neiva), L. gomezi (Nitzulescu), L. columbiana (Ristorcelli and Van Ty), L. evansi (Nuñez Tovar) and L. ovallesi (Ortiz). The man-biting activity of L. cirrita (Young and Porter) at the Providencia study area was summarized by Young and Porter (1974).

The Study Area and Its Climate

The Providencia study area (Fig. II-1)¹ is situated in a hilly and sparsely populated region of the east central portion of the Department of Antioquia, Colombia. Our studies were made in the area surrounding the Providencia hydroelectric plant (latitude 7°19'N, longitude 75°04'W) of Pato Consolidated Gold Dredging, Ltd. This region lies within the foothills of the northern slopes of the central cordillera of the Andes (Fig. II-2). The Providencia study area is drained by the Río Anorí and varies in elevation from approximately 400 to 800 m.

The Providencia hydroelectric plant lies approximately 25 kilometers south and 22 kilometers west of Zaragoza, an important early center of Spanish gold mining activity established in 1581. There is no evidence that any of the early Spanish settled in the hilly Providencia region, and the rapid, boulder strewn Río Anorí is unnavigable. Additional information about the history of the Providencia region is presented in Appendix A.

The steep slopes characteristic of large portions of the Río Anorí watershed have prevented large scale colonization of much of this region including the Providencia

¹The Roman numeral II precedes the table and figure numbers to conform with the format used for the final report of the interdisciplinary research program entitled "Association of Vertebrate Pathogens with Ecological Perturbation of Tropical Forests" under which this study was conducted.

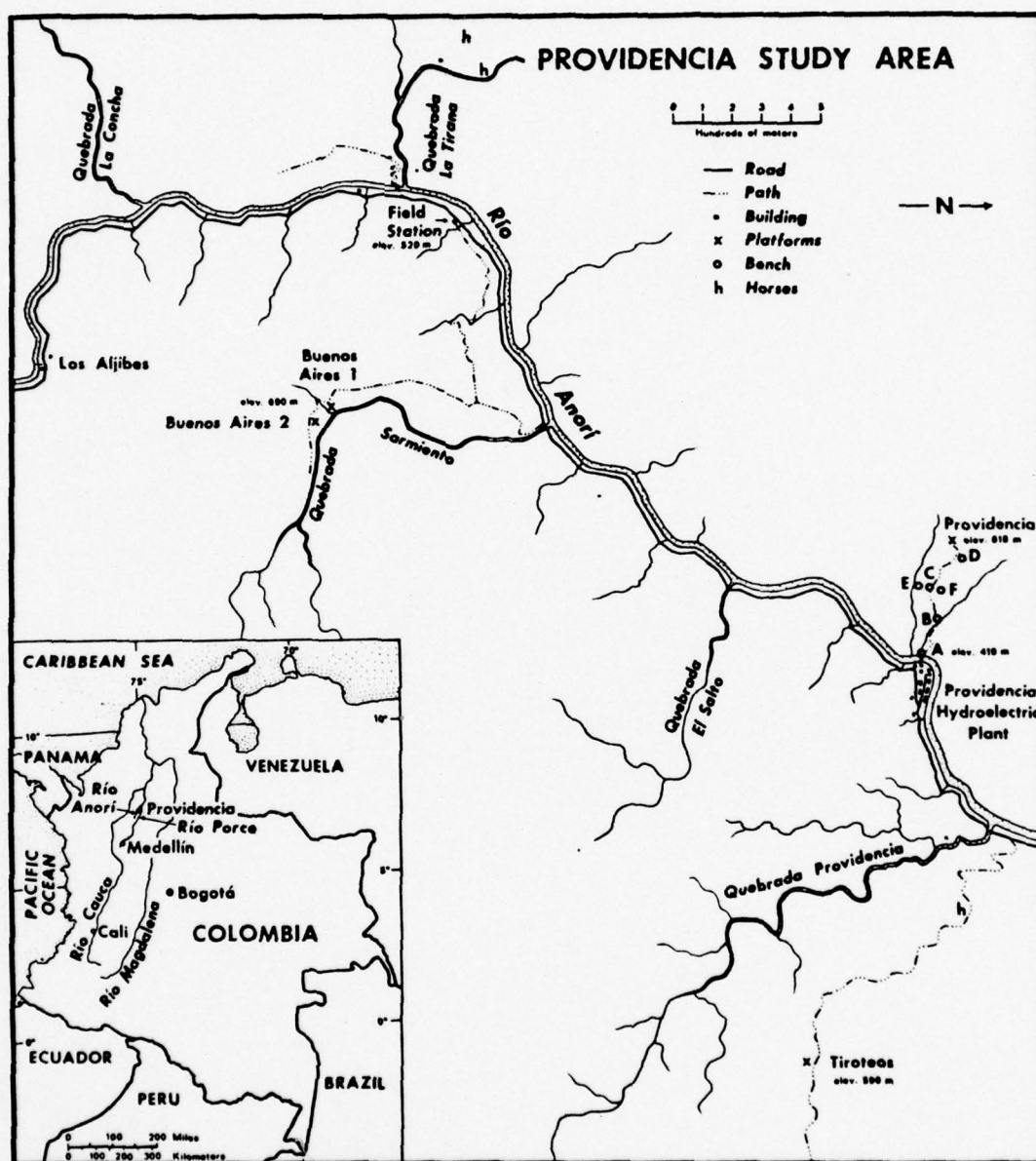


Fig. II-1

The Providencia study area and its location in Colombia.



Fig. II-2

The foothills of the northern slopes of the central cordillera of the Andes near the Providencia study area.

area. The hillsides facing the Río Anorí in the Providencia region are known to have been subjected to intermittent clearing since the 1930's and selective cutting since the 1900's. Large tracts of relatively undisturbed forest still exist and in general tend to become less disturbed as one moves away from the river. Relative inaccessibility and a very hilly topography have tended to discourage the use of the area for livestock production, although such an endeavor was being undertaken in 1971 near La Tirana. In addition to the 11 to 12 families associated with the Providencia hydroelectric plant, only a few subsistence colonos live in the Providencia region, and they reside primarily on the slopes facing the Río Anorí.

The Providencia region has a mean annual rainfall of 462 cm (Table II-1), and there is a distinct tendency for this rain to occur at night (Table II-2). A dry season, characterized more by a reduction than absence of rain, usually occurs from December through March. No month has a mean rainfall of less than 9 cm. Daily rainfall exceeded 10 cm on three occasions in 1970 and seven in 1971. The unusually large amount of rain recorded during the 1970-71 dry season occurred while our field studies were in progress and has perhaps minimized the influence this period may have on the population levels of the haematophagous Diptera. The nocturnal pattern of rainfall is thought to be related to the geographic location of the Providencia region in the

Table II-1
Monthly and annual rainfall (in cm) recorded at the Providencia hydroelectric plant.

Year	Month												Annual
	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
Mean ^a	13.5	9.4	19.8	35.3	59.9	54.6	46.2	61.7	46.2	51.0	47.2	17.5	462.3
1970	16.3	11.2	21.1	48.3	45.2	70.1	48.3	82.6	57.9	37.3	38.4	36.8	513.5
1971	36.3	27.2	50.5	24.6	53.3	43.2	53.8	57.4	69.6	60.4	54.6	11.2	542.1

^a Twenty-one year mean compiled from climatic records maintained at the Providencia hydroelectric plant by Pato Consolidated Gold Dredging, Ltd., for the years 1944-49 and 1957-71.

Table II-2

Hourly distribution of rainfall for the Providencia region.^a

Hour beginning	Observations	% Frequency of rainfall
01	41	34
02	45	24
03	45	33
04	45	31
05	44	34
06	0	--
07	120	13
08	121	6
09	121	7
10	121	4
11	121	2
12	121	0
13	121	2
14	120	3
15	120	4
16	113	8
17	43	2
18	46	11
19	46	11
20	47	13
21	48	15
22	48	19
23	44	23
24	42	33

^aCompiled from climatic data recorded during the temporal distribution studies of haematophagous Diptera in 1970-71. Rainfalls of shorter duration than 15 minutes were excluded.

foothills of the central cordillera. The percent frequency of rainfall for each hour of the day (Table II-2) was compiled to determine if there was a distinct temporal pattern of rainfall and should not be construed as a probability table.

A high annual rainfall which occurs primarily at night, an absence of a severe dry season, and a moderate elevation (400-800 m) all tend to promote a continuously high relative humidity in the Providencia region. A hydrothermograph was maintained from December 1970 through July 1971 in the clearing below the Providencia forest. This instrument was located just above ground level, beneath the bench at clearing site C. The mean monthly minimum relative humidities are presented in Table II-3. A mean monthly maximum relative humidity was not calculated since the values were consistently above 95% and thus in a range of limited accuracy (Grubb and Whitmore 1966).

In 1971 the mean maximum temperatures in the clearing for those months which normally comprise the dry season were somewhat lower than for the other months in which the hydrothermograph was maintained (Table II-3). Variation between months was somewhat smaller for the mean minimum temperatures than for the mean maximums. The lowest mean minimum temperature occurred in July. Hourly forest temperature means were compiled from readings obtained during the platform studies (Table II-4). The sharpest temperature

Table II-3

Meteorological data recorded by a hydrothermograph located
in the center of a clearing (bench site C).^a

Month	Temperature °C		Relative humidity %
	Mean maximum	Mean minimum	Mean minimum
1970			
December	28.4	21.1	72.4
1971			
January	27.4	21.1	73.6
February	27.5	21.0	73.0
March	26.7	21.8	79.4
April	28.1	21.3	76.0
May	28.7	21.6	71.8
June	29.5	20.8	66.2
July	29.1	20.1	67.4

^aThe hydrothermograph was situated just above ground
level beneath the bench.

Table II-4

Hourly forest temperature means for the Providencia region.^a

Hour	Observations	Mean
01	29	22.1
02	28	21.9
03	26	21.8
04	26	21.7
05	26	21.7
06	24	21.5
07	45	21.8
08	51	22.0
09	53	22.7
10	53	23.4
11	53	24.1
12	52	24.5
13	52	24.6
14	52	24.7
15	52	24.7
16	52	24.5
17	71	24.3
18	35	24.2
19	33	23.7
20	33	23.2
21	33	23.0
22	32	22.9
23	32	22.5
24	30	22.2

^aRecorded from a thermometer placed at a height of 0.7 m above forest floor during the temporal distribution studies of haematophagous Diptera in 1970-71.

changes within the forest occurred between 0800 and 1100 hours at which time the temperature increased about 2°C . A somewhat less pronounced corresponding decrease in temperature occurred between 1800 and 2000 hours. The temperature continued to fall slowly throughout the night, reaching a low at 0600 hours. The mean maximum temperature within the forest, based on 52 sets of observations taken over one year, was 25.2°C . A mean minimum forest temperature based on only half as many observations was 21.5°C . Temperatures at the Tiroteos site appeared to be about $0.5\text{--}1.0^{\circ}\text{C}$ higher than at the Buenos Aires sites. The latter site was 100 m higher in elevation. Temperatures at the Providencia forest site tended to be somewhat intermediate, more closely resembling the Tiroteos site.

Classification and General Description of the Forests in the Providencia Region

Since the Providencia region has an estimated mean temperature of 23.1°C , an annual mean rainfall of 462 cm, and an elevation varying from 400 to 800 m, the forest would be classified according to the Holdridge Life Zone Chart (Holdridge 1947) as Tropical Wet Forest, cool transition (Holdridge et al. 1971). Most of the forested areas occurred on steep, well drained slopes. For example, the terrain of the Buenos Aires forest in the vicinity of the first platform site was quite variable with the direction

of slope fluctuating from 60° east of north to 25° east of south and the angle of slope ranging from 19 to 70%. The soil of the Providencia region was derived from metamorphic parent material (Anon. 1969), and in the forests it tended to be acidic with low natural fertility.

On the basis of physiognomic characters, the forests of the Providencia study area tend to be rather intermediate between the Tropical Wet Forest and Tropical Premontane Wet Forest Life Zones (Holdridge et al. 1971). The Buenos Aires and Tiroteos forest sites had an upper closed canopy comprised of trees 22-30 m tall with occasional emergents to 35 m. The forest at the Providencia site appeared to be about 5-10 m taller. These heights are less than the 45-55 m tall upper canopy observed for the Tropical Wet Forests of Costa Rica by Holdridge et al. (1971) and are somewhat lower than that recorded for the Premontane Wet Forests. The difference in height may be attributable to the general steepness of the slopes upon which the forests of the Providencia area occur. However, the thicker trunks of large trees, large number of tree species, usually large number of palms, and limited distribution of tree ferns more closely align the forests of the Providencia region with the Tropical Wet Forest Life Zone. In addition to these characters, a generally sparse ground cover and relatively low density of epiphytic moss on trunks further distinguish the Providencia forests from the Tropical Premon-

tane Rain Forest Life Zone.

The estimated density of trees (10 cm dbh [diameter at breast height] or more), 78.5/0.1 ha (73.1/10,000 sq ft) at the Tiroteos site and 81.6/0.1 ha (75.9/10,000 sq ft) at the Buenos Aires site, was somewhat greater than that recorded for the Tropical Wet Forests of Costa Rica by Holdridge et al. (1971) but less than that observed by Grubb et al. (1963) for lowland rain forest in Ecuador. Species diversity was great at all sites, e.g., within a 242 m² sample area at the Tiroteos site there were 35 species, 14 of which had a dbh exceeding 10 cm. The upper canopy of these forests was composed of many species including: Anacardium excelsum Skeels, Caryocar costaricense Donn. Sm., Carapa guianensis Aubl., Dimorphandra pemigera Tul. Brosimum sp., Andira sp., and Ocotea sp. The understory of all three forests included representatives of such genera as Inga, Luehea, Miconia, Pouteria, Turpinia, and Xylopia. Leaf fall during the dry season was not readily apparent although one of the Caryocar costaricense at the Buenos Aires site became partially deciduous.

The composition of tree species forming the upper canopy varied with each forest and these floristic differences seemed to partially account for certain physiognomic variations between the forests. The frequent occurrence of Carapa guianensis in the Providencia forest resulted in buttresses being a prominent feature of that forest.

Buttresses were least noticeable in the Tiroteos forest where they were considerably reduced both in number and size. Herbaceous epiphytes and lianas were abundant on the upper and middle strata trees at the Buenos Aires study site. Bromeliads and Araceae were the predominant herbaceous epiphytic forms but ferns, orchids, and cyclanths were also common. Tank epiphytes were estimated to be about five times as numerous at the Buenos Aires site as at the south facing Tiroteos location. However, bromeliads were more conspicuous in the Tiroteos forest since many tended to occur at quite low levels on trunks, a phenomenon which may be attributed to the frequently more open canopy. Palms were most abundant in the Tiroteos forest where, with an estimated density of 1,529/ha, they were a conspicuous component of the understory. Some selective cutting for bridge ties is known to have occurred in the Tiroteos forest. An extended description of the forest vegetation, especially of Buenos Aires and Tiroteos sites, is given in Appendix B.

Forest Platform Sites

The series of platform collections were made at three different forest locations locally known as Buenos Aires, Providencia, and Tiroteos (Fig. II-1). The distance between the Providencia and Tiroteos sites was approximately 1.8 km while that between the Buenos Aires and Tiroteos

sites was about 2.7 km. The latter two locations were united by a vast expanse of forest extending unbroken for many kilometers to the east.

Two platform sites were constructed in the Buenos Aires region, but only one, Buenos Aires 1, was used for the night studies. Both of these sites were located in a small extension of undisturbed forest that merged to the south and west with secondary forest on the steep slopes facing the Río Anorí. To the east undisturbed primary forest extended continuously for many kilometers. Approximately 200 m to the north of the Buenos Aires 1 site, there was a 3.5 hectare fern-shrub thicket. This area was cleared in 1937 and was maintained as a pasture until abandonment in 1951. Portions of this clearing have been intermittently burned since then.

The Buenos Aires 1 platform site (Fig. II-3) occurred on a narrow ridge near the top of a steep southeast facing slope at an elevation of 690 m. A small creek passed within 20 m of the site and joined a rapid stream about 50 m away. The understory and canopy platforms were constructed in separate trees of Caryocar costaricense Donn. Sm. which were 9 m apart. These platforms were at heights of 6.4 m (21 ft) and 16.2 m (53 ft). The tree containing the upper platform was 27 m tall, and the crown of both trees supported a heavy load of herbaceous epiphytes including many large bromeliads.



Fig. II-3

The understory platform at the Buenos Aires 1 forest site.

About 90 m to the southeast and at the same altitude a second platform site, Buenos Aires 2, was constructed on a steep, approximately 50° , north facing slope. A 15 m wide clearing for power lines passed through the forest within 30 m of this location. The platforms were built in a tree known locally as "granadejo" and were at heights of 4.3 m (14 ft) and 13.4 m (44 ft). Unlike the platform trees at the Buenos Aires 1 site, the crown of this tree did not have a profuse growth of herbaceous epiphytes.

The Providencia platform site (Figs. II-4 and 5) was located on a steep east facing hillside overlooking the hydroelectric plant at Providencia (Fig. II-6). The lower two-thirds of this hillside was first cleared between 1941 and 1943 and now contains several vegetative formations including pasture, mixed pineapple-plantain cultivation, and secondary forest. This area will be described in more detail later in relation to the clearing sites. A slightly disturbed primary forest extended along the upper one-third of this hillside, but the west facing slope had recently been cleared for pasture. The forest was only about 200 m wide above Providencia but became more extensive to the southwest, reaching the river in several locations.

A platform site was constructed within the Providencia forest about 50 m from its lower margin with the clearing. The elevation at this level was 618 m, and the slope was gentle, about 20° , although most portions of the hillside



Fig. II-4

The canopy platform at the Providencia forest site.



Fig. II-5

The forest floor at the Providencia forest site, including the base of the tree in which the platforms were built.

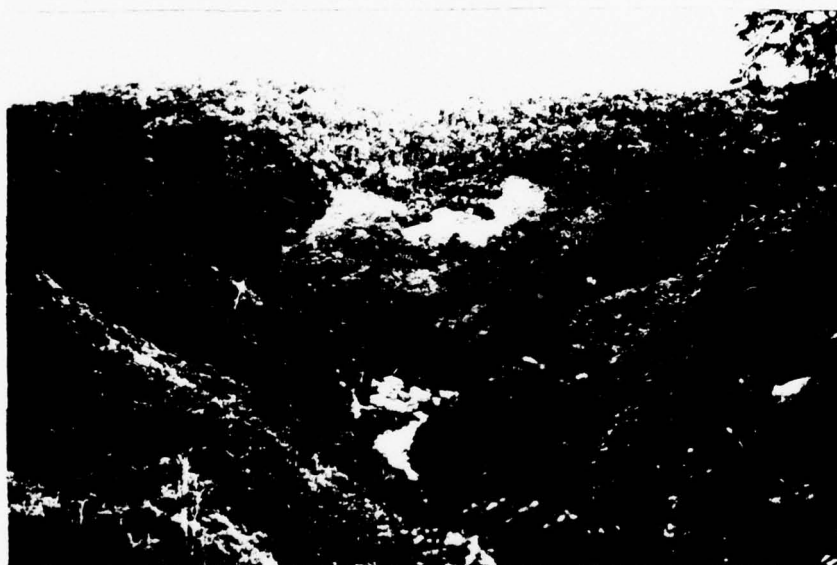


Fig. II-6

The Río Anorí valley at the Providencia hydroelectric plant. The clearing (bench) sites were located on the hillside in the background and the Providencia platform site was located in the forest above the clearing.

were steeper, varying from 45° to 70° . The platforms were built in a buttressed, 39 m tall Carapa guianensis Aubl. at heights of 6.6 m (21.5 ft) and 18.6 m (61 ft). Only a few herbaceous epiphytes occurred in the crown of this tree.

Early differences in the populations of haematophagous Diptera observed between the Buenos Aires and Providencia locations prompted the construction of a platform site in a third forested area known as Tiroteos. This platform site was situated about 1 km inside an extensive tract of forest which merged with the Buenos Aires forest and extended for many kilometers to the east. The platforms were built in a large Dimorphandra pemigera Tul. (J. S. Denslow, personal communication) which was located close to the top of a steep, approximately 45° , south facing slope at an elevation of 590 m. With an estimated height of 27.4 m this tree was a constituent of the upper canopy but had only a few herbaceous epiphytes and none of these were tank bromeliads. The platforms were placed at heights of 6.4 m (21 ft) and 18.0 m (59 ft).

Clearing Sites

All six of the clearing sites were located in the extensive open area below the Providencia forest platform site (Fig. II-6). This area, located on the eastern slope of the hill directly across the Río Anorí from the Providencia hydroelectric plant, was originally cleared between

1941 and 1943. Various portions of this hillside have been used in a variety of ways so that several kinds of vegetative formations were present at the time of our study. The collecting sites were so arranged as to occur in these major vegetative formations. Four of the six collecting sites, A through D (Fig. II-1), were placed at approximately 60 m altitudinal intervals beginning with site A at the base of the hillside adjacent to the Río Anorí. Sites E and F were located at the same altitude as site C but were situated at the southern and northern edges of the clearing, respectively. Each of these collecting locations contained a bench shaded by a thatched roof; hence, they were referred to as bench sites.

Bench site A, elevation 420 m, was situated next to the Río Anorí across from the Providencia hydroelectric plant. This site was at the edge of a wooded area which extended uphill to the west. This woods was comprised of trees, including Cecropia spp., ranging in height to 12 m and had a thick undergrowth. The bench site was shaded after 1400 hours. The site was about 8 m above the river bed and faced 80° east of north toward several houses 150-200 m away. A fast flowing creek emptied into the Río Anorí about 12 m upstream.

Bench site B, elevation 470 m, occurred in an area of diverse cultivation (Fig. II-7) approximately 120 m west-northwest of site A. To the north, a large cleared area



Fig. II-7

An area of diverse cultivation in which clearing (bench) site B was located. Note the dense growth of pioneer vegetation among the plantains and fruit trees.

planted with corn (Zea mays L.) extended to within approximately 40 m of the site, and a small creek passed within 12 m to the northeast. In October 1970 a clearing, about 55 x 65 m, was made just to the south of the bench site and was planted with corn and pineapple (Ananas comosus Merr.), but by August 1971 many herbaceous pioneer species had become established, producing a very thick growth to a height of 2 m. A small creek passed along the southern margin of this clearing. The bench site itself was located within a small grove of diverse fruit trees but some plantains (Musa paradisiaca L.), yucca (Manihot esculenta Crantz.), and pineapples were also present. The bench was constructed beneath a zapote tree (Matisia cordata Humb. and Bonpl.) which shaded the site throughout the day. An extensive area of plantain cultivation extended for about 80 m to the west. Some plantain and pineapple cultivation occurred to the east but soon merged into a thick growth of pioneer and early secondary vegetation. Secondary forests with broken canopies and trees from 6-16 m tall occurred along the outer margins of large portions of the cultivated areas.

Bench site C, elevation 540 m, was situated centrally in the lower half of a pasture, approximately 110 m west-southwest of site B. This site was fully exposed although there was a small clump of trees about 35 m to the west near the center of the pasture. An area of plantain cultivation occurred approximately 30 m to the east of the bench

site. About 40 m north of bench site C the pasture merged with an extensive area of pioneer vegetation, and a 10-15 m tall early secondary forest (Budowski 1965) was located 40 m south of the bench site. The vegetation of the pasture consisted primarily of grasses and some herbaceous dicots and frequently reached a height of 1 m.

Bench site E, elevation 540 m, was located to the south of bench site C. It was situated just within the pasture at its margin with the 10-15 m tall early secondary forest. In the late afternoon the bench site became shaded by the forest. About 15 m to the south of the bench site a rapid creek passed through the secondary forest. This forest merged about 100 m to the west with the mature forest containing the Providencia platform site.

Bench site F, elevation 540 m, was situated about 40 m to the north of bench site C and was at the edge of the pasture and a strip of late pioneer vegetation ranging in height to 9 m. The rather narrow, sinuous band of pioneer vegetation extended upward to the forest margin about 130 m to the west. A small creek passed bench site F about 65 m to the northeast and pioneer vegetation grew on the steep slope between this bench site and the creek. Bench site F, like site C, was thus not shaded by trees.

Bench site D, elevation 600 m, was located at the extreme northwest edge of the pasture, adjacent to the tall, mature forest containing the Providencia platform site.

The bench site was situated at the tip of a small protrusion of the pasture into the forest. It was thus surrounded on three sides by forest and consequently was shaded by early afternoon. One creek passed approximately 90 m to the southwest of this bench site and a second, about 110 m to the southeast. The forest platform site was about 40 m to the southwest of this bench site.

The location of the bench sites may be summarized as follows: site A, edge of river and early secondary woods; site B, area of extensive and diverse cultivation; site C, open pasture; site D, edge of pasture and mature forest; site E, edge of pasture and early secondary forest; site F, edge of pasture and pioneer vegetation extending from forest. Since all of the sites were situated on the eastern slope of the hillside, they became shaded in the late afternoon when the sun passed behind the top of the hill.

MATERIALS AND METHODS

Collecting Methods and Number of Catches

Collecting methods. At each of the three forest platform sites six men were employed. This permitted the simultaneous collection of biting Diptera by two men at each of the three levels. The two-man teams rotated between the canopy, understory, and ground level at 2-hour intervals in order to minimize the effects of difference among workers both in their attractiveness to the Diptera and in their collecting ability. Kettle and Linley (1967) and Kettle (1969) have shown that substantial differences may occur between workers in their attractiveness to Ceratopogonidae, and they have calculated correction factors for each worker. We did not attempt to determine such differences between workers since it was not possible to retain the same six collectors throughout the period of this study. While collecting, the workers wore short sleeve shirts, rolled their pants up above their knees and did not wear shoes. All specimens landing on the workers were collected individually in either 1-dram or 5-dram vials, depending upon the size of the insect. To relate the

specimens to the capture site, level, and time of collection, at the end of each catch period at each level all of the vials containing specimens were placed in a plastic bag labelled with the date, catch period, and level. For the night catches each collector used a flashlight which had its front glass covered with red cellophane to minimize the attraction of insects to light. After a platform collection had been completed the specimens were refrigerated at the field laboratory. At weekly to biweekly intervals the specimens were shipped with ice in insulated styrofoam boxes to the Medellín laboratory.

Duration and number of catches. Numerous workers studying the periodicity of biting activity of haematophagous Diptera (Lumsden 1952, Kettle and Linley 1967, Chanio-tis et al. 1971b) have related the time of their collection periods to sunrise and sunset. Haddow (1954) has shown the value of obtaining an activity profile corresponding to the 24 hours of the day while at the same time maintaining similar light intensity relations (see Williams 1939) for each of these periods throughout the year. Hence, at the latitude of Providencia, $7^{\circ}19'N$, the time period between sunset and sunrise was divided into 12 periods of equal duration as was the period between sunrise and sunset. These periods usually differed in length from the normal 60-minute hour. Such a division insured that the times of sunrise and sunset and their accompanying rapid changes in

light intensity did not fall into two different catch periods at different times of the year. The times of sunrise and sunset for the latitude and longitude of Providencia were obtained from a table prepared for us by the Nautical Almanac Office, U.S. Naval Observatory, Washington, D.C. The time of sunrise in the Providencia region varied from 0542 to 0619 hours, and the time of sunset varied from 1739 to 1821 hours. The maximum length of each daylight catch period was 63 minutes and the minimum was 58.5 minutes; conversely, the maximum length of each night catch period was 61.5 minutes and the minimum was 57 minutes.

The series of forest night catches upon which the phlebotomine sandfly study is primarily based began with a collection in late July 1970 at the Buenos Aires 1 site. This was followed by two collections per month for the remainder of the year. One of these collections was made each month at the Buenos Aires 1 site while the other collection alternated between the other two sites. In 1971 a collection was made at each of the three sites every month through August. In addition, 58 daytime forest catches were made between May 1970 and July 1971. A series of 12 night catches was made between March and August of 1971 in a clearing adjacent to the forest in which the Providencia platform site was located. An extensive series of 65 daytime catches was also made in this clearing from October 1970 to August 1971.

The diurnal platform collections were 10 catch periods in length, extending from approximately 0700 to 1700 hours. The nocturnal collections extended from 1700 to 0600 hours and thus included the last day catch period in addition to all 12 night periods. The first daylight period, approximately 0600 to 0700 hours, was not sampled since it would have been necessary either to extend the already excessively long night collections or have the workers reach the relatively remote platform sites in the dark over difficult uphill trails. Continuous collections for 24 or more hours similar to those of Haddow (1954) were economically unfeasible.

Although heavy rains were infrequent during the day, they were of common occurrence at night during the rainy season and often prevented collecting on the exposed platforms for portions of the night. The decision to stop collecting during periods of heavy rain rather than construct roofs over the platforms was made primarily on account of the severe lightning that frequently accompanied these rains. Catch periods in which heavy rains occurred have been excluded from the data used to calculate the means. Since the bench sites had roofs, rain did not interrupt any of the collections made in the clearing.

Clearing catches. Although there were a few differences, the general procedure used for the clearing catches was similar to that for the forest studies. The catches

in the clearing were all conducted at ground level and were made by the same six collectors that participated in the forest studies. To facilitate comparison with the forest series of catches, the collectors worked in pairs, and this resulted in the simultaneous sampling of three sites. Therefore, the clearing collections were made on two consecutive days with sites A, B, and D being sampled on the first day. Aspirators were used in making the night collections, and all specimens were chloroformed and preserved in 70% ethanol.

Collection of resting adults from the base of trees.

From November 1970 to June 1971 a series of collections was made of phlebotomine sandflies resting at the base of 11 trees in the forest containing the Providencia platform site. This portion of the forest was situated on a steep slope facing the Río Anorí. The collections were made once a month although only a few of the sites were sampled in December. Resting adults were collected with aspirators in a manner similar to that described by Chaniotis et al. 1971a. An attempt was made to collect all of the specimens resting on the trunks from ground level to 1.5 m. The adults tended to be congregated in the most sheltered area of the tree base which was invariably located on the downhill side. On a few of the trees, these protected areas became damp after heavy rains and few if any sandflies could be found. Trees 4 to 7 and 10 and 11 were buttressed,

35 to 40 m tall specimens of Carapa guianensis. Trees 6, 7, and 11 had immense buttresses. The remaining trees, 1 to 3 and 8 and 9, were of several different species and had fluted or mildly buttressed trunks. The first three of these trees were between 25 and 30 m tall and trees 8 and 9 were 35 to 40 m tall.

Species Identification

The majority of the Phlebotominae obtained from the platform collections were separated into groups for attempted virus isolation based on their external appearance. Since these superficial groupings often contained more than one species, we also cut off the posterior abdominal metameres containing the spermathecae. These metameres were stored in appropriately labeled shell vials containing a mold inhibitor. After returning to Wisconsin, the pooled specimens were identified by clearing the metameres in 10% KOH and examining the spermathecae in a depression slide containing lactophenol tinted with iodine. In addition, representative specimens from each collection along with any unusual specimens were preserved by layering in pillboxes. All of the specimens taken from the clearing sites were preserved in alcohol. These specimens were more satisfactorily cleared by placing them in beechwood creosote for 2 days before they were cleared in 10% KOH.

External morphological characters and color patterns were used by us to group or distinguish the specimens in the biting catches, although the specific identification of each species was ultimately based on their spermathecae and other structures requiring high power magnification. Chaniotis (1974b) has recently outlined the problem of identifying phlebotomine sandflies on the basis of external characteristics and has provided a key to separate the anthropophilic species in Panama.

Warileya rotundipennis Fairchild and Hertig was readily distinguished from the other man-biting species by its distinctive wing shape and uniformly tan appearance. L. olmeca-bicolor Fairchild and Theodor was identified by its very distinctive color pattern (Chaniotis, 1974b). The combination of pale wing scales and infuscated mesonotum distinguished L. hartmanni from the other common man-biting species. Although L. cirrita resembled L. hartmanni in external appearance, it was recognized by its large size and paler mesonotum. L. osornoi (Ristorcelli and Van Ty) was another vexator group species that was occasionally taken in the biting catches. Superficially, this species is very similar in appearance to L. hartmanni although the longer fifth palpal segment permits its separation under high power magnification. Careful examination of eight forest catches which had been preserved in their entirety and all of the clearing catches indicated that this species

was rare, but undoubtedly a few have been misidentified as L. hartmanni.

L. trapidoi and L. yuilli were readily distinguished from the other common species by their pale mesonotums, grey wing scales, and small size. However, we were unable to distinguish these two species by external appearance. Since L. trapidoi and L. yuilli were not distinguished in the first three night collections, these collections were not included in the tabulations of these two species. A total of 645 specimens of these two species, the majority of which were engorged, were not identified, and thus it was necessary to apportion these specimens to the period in which they were caught according to the ratio of known specimens in that catch period. A final group characterized by an infuscated mesonotum and dark wing scales was comprised of L. panamensis, L. tintinnabula Christensen and Fairchild, L. gomezi, and L. bifoliata Osorno-Mesa, Morales-Alarcón, de Osorno, and Muñoz de Hoyos. Subsequently we were able to separate these species according to the length of their fifth palpal segment and the color of the pronotal lobes. L. gomezi and L. bifoliata have long fifth palpal segments; whereas L. panamensis and L. tintinnabula are members of the subgenus Psychodopygus and have very short fifth palpal segments. The pronotal lobes of L. tintinnabula and L. gomezi were almost white while those of the other two species were infuscated and concolorous with

the mesonotum.

Data Analysis

Logarithmic transformations. Logarithmic transformations (\log_e) of actual catches were frequently used in the analyses presented in this paper. The antilogarithm of the arithmetic mean of logarithms of a set of numbers is the geometric mean of these numbers. Since the catch of a particular species sometimes was zero, $\log (x + K)$, where K equals some constant, was used instead of $\log(x)$ to avoid the problem of $\log(0) = -\infty$. When there was a conversion to antilogarithms the constant (K) was subtracted from the antilogarithm. The result is close to the geometric mean provided that a relatively small constant is used. The use of logarithmic transformations for the analysis of biting cycles has been discussed by Haddow (1954). Insect catches tend to be quite variable in magnitude and between catch differences are often of a multiplicative (geometric) nature (Williams 1937, 1951). Through the use of the geometric mean, the influence of very large catches is reduced since the proportion $\frac{\log x}{x}$ decreases with increasing size of x where x is any number greater than 3.

In many of the tables summarizing the catches, the results were presented both as absolute numbers and as modified geometric means. Individual catches were transformed to logarithmic values (Haddow 1954, 1960). The

terminology of Haddow (1960) and Kettle and Linley (1967) has been adopted for those portions of the study where the additive constant was consistently 1.0. The symbol M_L represents the mean log catch:

$$M_L = \frac{\sum \log(x+1)}{n}$$

where n is the number of observations. M_W represents the modified geometric mean: $M_W = (\text{antilog } M_L) - 1$. In this paper M_W is the modified geometric mean catch per period. $\log(x+1)$ has the desired effect of resembling a square root transformation for numbers up to 10 and being similar to $\log(x)$ for greater values (Steel and Torrie 1960). The modified geometric mean catch per night for a given site and level was used for the statistical analyses.

Temporal patterns. The graphs of the summary temporal patterns of biting activity were constructed from the modified geometric means of the catch periods (M_W). These means were reduced to percentages (Haddow 1960) to facilitate comparison of the temporal patterns between both species and habitats. When the temporal pattern of biting activity was partitioned by vertical level (Fig. II-20), the modified geometric means were not reduced to percentages as we were interested in the magnitude of the differences between levels.

The graphs of the temporal patterns for individual

nights were derived by converting the number taken during each catch period to a percentage of the entire night's catch. Averaging techniques such as running means or the modified geometric mean of the three vertical levels were not used as they frequently caused excessive distortion of these temporal patterns.

As mentioned earlier, the night catches consisted of 13 consecutive periods and included the last day catch period. Although phlebotomine sandflies were seldom encountered during the last day catch period, it is included in the tables and graphs of the temporal patterns of biting activity but is omitted from the other tables concerned with nocturnal biting activity and from the statistical analyses.

Between-site analyses of the clearing catches. A small series of night catches was made at the six clearing sites to provide an indication of Phlebotominae man-biting activity in a variety of vegetative formations located at varying distances from the forest. First, the null hypothesis of no difference in biting activity between the clearing sites was tested for each of the six most abundant species and for the entire population. A two-way analysis of variance with a randomized complete block design was computed for each of the species and for the entire population. Differences between catches may be of a geometric rather than additive nature (Williams 1951). Since the

standard analysis of variance model assumes the components of the variance are additive, the precision of this analysis is likely to be reduced if they are multiplicative. Therefore, Tukey's test of non-additivity (Snedecor and Cochran 1967), in conjunction with some preliminary two-way analyses of variance, established the necessity of a logarithmic transformation to produce additivity. Along with additivity, the logarithmic transformation tended to bring about a closer approximation to normality and equality of variance. To avoid the problem of zero values, a constant of either 1.0 or 0.1 was added to each of the values used in the analyses before the transformations were made. The constant used for a given species was also determined by Tukey's test of non-additivity. The observations used in the analysis of variance for a given species were thus the transformed sums of the specimens taken on each of the nights at each of the sites.

For those species with statistically significant site F ratios, $P \leq 0.05$, all 15 simple differences between sites were tested for significance as was the contrast between the two forest margin sites, D and E, and the four sites within the clearing. The multiple comparison method of Scheffé was used as it allows one to make every contrast of interest without increasing the probability of declaring a contrast significant when it is not (Miller 1966, Nemenyi 1968). This test may be expressed as

$$\frac{\sum c_i \bar{x}_i}{\sqrt{\sum \frac{c_i^2}{n_i}}} \hat{\sigma}^2$$

where the c_i 's are linear coefficients which add up to zero, $\sum c_i = 0$; the \bar{x}_i 's are the means to be tested; n_i denotes the number of catches in the category whose mean is \bar{x}_i ; and $\hat{\sigma}^2$ is the estimated variance. In those instances in which the contrast between the two groups of means, i.e., D + E vs A, B, C, and F, was significant, confidence limits were constructed according to the method of Scheffé. The confidence intervals of all contrasts have half-lengths $SE\sqrt{(k-1)F_\alpha}$ where SE is the estimated standard error, k represents the number of means which can be compared, and F_α denotes the critical value of F for a desired probability with degrees of freedom from the analysis of variance for the means being tested and error (Nemenyi 1968).

For each species the pattern of its biting activity across the six clearing sites was compared with the pattern of each of the other five prevalent species. The abundance of each of these species in relation to each of the others was also determined. Again, two-way analyses of variance with randomized complete block designs were used, but the analyses were made on log ratios, i.e., the log transformed sum of specimens of one species taken from a given night and site minus the log transformed sum of

another species for the same night and site. Thus, the analysis of variance F ratio for testing equality of site means becomes a test for interaction between species and sites and detects whether there is a significant difference between the patterns of biting activity of any two given species across the six sites. In other words, a significant F ratio indicates that the abundance ratio of the two species fluctuated significantly between sites. When the F ratio was significant, 95% confidence intervals based on the t-distribution were calculated for the abundance ratios of each site, providing an indication of the relative abundance of one species to another. Allowance could be made for the multiple comparisons, i.e., six comparisons for the above instance, that would widen the confidence intervals. However, these comparisons are between means of catches made in the field under the influence of a number of undefined environmental and physiological variables so that an allowance for multiple comparisons would be of doubtful value. A single confidence interval for all sites was calculated when the F ratio for interaction between sites and two species was not statistically significant. In computing this confidence interval, the total mean square was used as an estimate of variance. The main effect F ratio indicated whether there was a significant difference in the amount of biting activity between any two species. The 95% confidence interval for all sites

included 1.0 (ratio 1:1) whenever the main effect F for difference in abundance was not statistically significant.

Estimates of the diversity and evenness of man-biting activity. The degree to which the various species of phlebotomine sandflies were attracted to a human host is not known. Thus estimates of sandfly diversity at the six clearing sites cannot be made from the catches. However, estimates of the diversity of the biting activity at the various sites can be made using

$$\hat{H}' = - \sum_i \frac{X_i}{\sum_i X_i} \log_e \frac{X_i}{\sum_i X_i}$$

where X_i is the total catch of species i over all the observations. This formula gives a biased (statistical sense) estimate of H' but it is satisfactory for the purpose of comparing diversity of biting activity between the six clearing sites.

The evenness or equitability index J' (Pielou 1969) was used as it appears to be less dependent than other measures on the observed number of species when the number is small, especially when it is less than ten (Sheldon 1969). The number of species taken at the six sites varied from 6 at site A to 11 at site E.

Between-level and between-site analyses of the forest catches. Analysis of the night forest catches has been complicated by missing observations which were primarily caused by interruptions in collecting due to heavy rains. As a result, the 12 catch periods have unequal numbers of observations. Since catches in the forest were conducted

simultaneously at three levels, they were all discontinued at the same time; thus an equal number of catch periods was maintained for each level. Catches were made at only two forest sites per month from September 1970 to December 1970, resulting in an unequal number of catches between the sites.

The null hypothesis of no difference in man-biting activity between the three forest levels was tested by means of a nonparametric rank test for comparing all possible pairs of treatments (Wilcoxon and Wilcox 1964). Briefly, for p treatments and n repetitions of the p treatments, rank numbers are assigned for each p of a given repetition. In our case, 0 was assigned to the smallest value and a rank of 2 was given to the largest. The assignment of ranks is repeated n times. The sum of the ranks for each treatment is obtained and all possible differences among these sums are computed. For n 's of 25 or less, these differences may be compared with critical differences associated with specific probabilities in a table (Wilcoxon and Wilcox 1964). Alternatively, these differences for any n may be divided by their standard deviation and compared with a table of critical values for rank sum tests adjusted for making any and all comparisons among several means (Nemenyi 1962). The degrees of freedom used are "very many" because of known variance. The standard deviation of a difference between three ranks may be expressed as $\sigma_d = \sqrt{2np(p+1)/12}$ which reduces to $\sqrt{2n}$. The

occurrence of ties is not assumed with this standard error formula, although a good approximation is achieved when only a few are present. To minimize this problem, we omitted those instances in which all three levels of a given repetition were zero.

The null hypothesis of no difference in man-biting activity between the three forest sites was tested for all species combined and for L. hartmanni, L. trapidoi, and L. yuilli. An analysis of variance with a factorial design was computed for each of these three species and for the entire population. These analyses were complicated by an unequal number of observations both between catch periods and between sites. To reduce the amount of missing data, i.e., the number of catch periods with missing observations, only the first seven catch periods were used for the analyses. This diminished the percentage of catch periods with missing observations from 22% to 13%. Missing observations in the last five catch periods were especially numerous for the Buenos Aires 1 site where values were present for only half of the periods. When an observation was missing from one or more of the first seven catch periods, the mean of the values present was computed. This mean was then substituted for those catch periods with missing observations. When observations were missing they varied from one to three, although there was an instance where four and another where five observations were absent. The creation

of a mean from six values on some occasions and from five or four on others does introduce an additional source of error into the analyses.

A general analysis of variance program, NWAY1, from the STATJOB series available from the University of Wisconsin-Madison Academic Computing Center was used for the analyses. The number of catch nights for the forest studies varied by site so that there were 14 for Buenos Aires 1, 11 for Providencia, and 10 for Tiroteos. For instances like this where there are an unequal number of replicates between cells, NWAY1 does an approximate unequal cell analysis using Scheffé's approximation.¹ The number of catch nights used for the analyses of L. trapidoi and L. yuilli were reduced by two for the Buenos Aires 1 site and by one for the Providencia site. The transformation $\log_e(X+1)$, where X is the sum of the seven catch periods, was applied to each replication before the analyses of variance were performed.

Comparisons between sites were made from the transformed site means for each level and for the three levels combined. The multiple comparison method of Scheffé was used for making the contrasts between pairs of means as it provides extra allowance for selection in multiple com-

¹Henry Scheffé, The Analysis of Variance (New York: John Wiley and Sons, Inc., 1959), p. 362-63.

parisons. This test has already been described in relation to the clearing data. The estimate of variance required for this method was the mean square variation within cells from the analysis of variance. The Scheffé critical values of t were derived from $\sqrt{(k-1)F_{\alpha}}$ where k is the number of means which can be compared and F_{α} denotes the critical value of F for a desired probability with degrees of freedom from the analysis of variance for site and variation within cells (Nemenyi 1968). Since the comparisons between sites were made for each of the three vertical levels, the critical values of F used in the above formula were $\alpha = .05/3$ and $\alpha = .01/3$. This allowance, derived from the Bonferroni inequality, was made to insure that the error probability per analysis did not become greater than .05 (Nemenyi 1968). This allowance was not used for calculating the Scheffé critical values for the comparisons for all levels combined. For these comparisons the critical values of F were $\alpha = .05$ and $\alpha = .01$.

The analyses of variance computed from NWAY1 (Table II-29) also provide an F ratio for levels. However, multiple comparisons between levels were not made since such comparisons have already been tested by the nonparametric rank method described earlier.

Polar ordination analyses. In an attempt to better understand the distribution of the man-biting Phlebotominae species over the variable microenvironments sampled and to

show the relationships of these environments from the standpoint of the Phlebotominae population, a polar ordination analysis of the Bray and Curtis (1957) type was applied to the series of night catches made at the forest and clearing sites. Over the past 10 to 15 years, polar and principal component ordination techniques have become widely used in the analysis of plant communities (Beals 1973). Helpful introductions to these methods are presented by Allen and Skagen (1973), Orloci (1966), and Anderson (1971).

Ordination techniques position a series of points, which may represent species, samples, or environmental factors, in an N-dimensional abstract space utilizing geometric principles. The dimensional framework may likewise be species, samples, or environmental factors so that a number of species may be placed as points in sample space or a series of samples may be placed as points in species space. The distances between a series of points in an N-dimensional space is a measure of their differences. When the multi-dimensional space is reduced to one, two, or three dimensional space for the purposes of simplification, clarification and graphing, a certain amount of variation, i.e., information, is lost. However, the new axes are chosen to minimize loss of ecological information.

In the present study 132 entities (catches) are considered. The series of 32 catches made in the forest over

a year's time were separated by level, thus accounting for 96 of the entities. The remaining 36 represent the catches made in the clearing between March and August of 1971 as previously described. The eight most abundant species (attributes) were used to characterize the entities. A sum for each of these species was obtained for a night's catch at a given site. These sums were transformed to square root values in order to reduce the influence of L. hartmanni which accounted for over half of the specimens taken. Considerable ecological information about an entire system may be derived from certain indicator species (Allen and Skagen 1973) which may not be the most abundant. Since the catches were not all of equal duration, the eight square root values of each entity were relativized, giving the percent contribution of each species to the total catch which sums to 1.0.

Intercatch distances were calculated from the dissimilarity measure $1 - 2w/(a+b)$. This distance measure is based on the coefficient of similarity $2w/(a+b)$ used by Bray and Curtis (1957) where a is the quantitative scores of species in one entity, b is the quantitative scores of species in another entity, and w is the lesser quantitative score of species common to both entities. In this analysis the dissimilarity measure actually becomes $1 - w$ since after relativization the total score of each entity was 1.0. Beals (1973) has reviewed the objections to the use of this

distance measure and has concluded that the results obtained from a Bray and Curtis type of ordination using the above distance measure have been more ecologically informative than those obtained from more sophisticated methods such as principal components analysis.

Once the intercatch distances have been calculated an axis is constructed on which the entities are positioned. The entities chosen as endpoints for the first axis could be those with the greatest intercatch distance which is essentially the method used by Bray and Curtis (1957). Since ecological information may be obscured by the influence of unusual stands when this method of endpoint selection is used, Beals (1973) has suggested that different criteria for endpoint selection, such as using two dissimilar entities with large variance in their distances with other entities, may be more appropriate. Thus, in the method used by us, the entity chosen as the first endpoint was the one whose matrix of distances from the other entities had the greatest variance. Before the variance of each entity's distance matrix was computed, zero values were removed from the matrix. In determining the second endpoint, a regression of the distances of a given entity to all other entities was made against the corresponding distances from the first endpoint. This was repeated for each of the other entities and the entity with the lowest regression coefficient was selected as the second endpoint.

The method of Bray and Curtis (1957) and Beals (1960) was used for the orthogonal projection of the entities onto the first axis.

The construction of the second and third axes was accomplished by using residual distance matrices as suggested by Beals (1973). The distance between two entities on the first axis represents an orthogonal component of the entire intercatch distance between these two entities. The remaining orthogonal component, i.e., the residual distance, can be determined from the Pythagorean theorem as follows:

$$h_j = [d_{1j}^2 - (x_{1j} - x_{2j})^2]^{\frac{1}{2}}$$

where d_{1j} is the distance between the two entities (for computing residual distances from the first axis, this is the intercatch distance derived from the dissimilarity measure) and the hypotenuse of a triangle with $x_{1j} - x_{2j}$ as the base and h_j the side. The base, $x_{1j} - x_{2j}$, is the distance between the two entities on the first axis, and h_j is the residual distance and lies perpendicular to the first axis. A residual distance (h_j) is calculated for every possible pair of entities and thus a residual distance matrix is created for each entity. The residual distances were used for selecting endpoints of the second axis and for the orthogonal projection of the remaining entities onto that axis. The methods of endpoint selection

and orthogonal projection were the same as those used for the first axis. The third axis was similarly constructed from a new set of residual distance matrices derived from the second axis. This process can be repeated to give as many additional axes as desired. Each new axis is constructed from the residual distance matrices of the preceding axis. The methods of endpoint selection and axis construction used in this study have been described and rationalized by Beals, Riechert and Will-Wolf.²

The coordinates for graphically positioning the entities in two or three dimensional space were derived from the axes used in the dimensional framework. When an entity is projected onto an axis, its distance from the base endpoint is its coordinate for that axis.

After the entity ordination was completed an ordination of the attributes (species) was made. Both ordinations were performed on a Univac 1110 using two programs, Bray and Curtis type ordination and graphic ordination plotting routine, graciously loaned to us by the University of Wisconsin plant ecology laboratory.

²E. W. Beals, S. E. Riechert, and S. Will-Wolf. The use of ordination in the analysis of niche space. Manuscript submitted to J. Anim. Ecol.

PHLEBOTOMINAE

RESULTS

Summary of the Common Species Taken
in the Forest and Clearing Catches

The species which occurred most frequently in the biting studies are listed in Table II-5. This table also gives the total number taken and a modified geometric mean for each of these species in both the forest and the clearing series of night catches. L. hartmanni, L. trapidoi, and L. yuilli accounted for 91% of the specimens taken in the series of forest night catches; and L. hartmanni, L. gomezi, L. yuilli, and W. rotundipennis accounted for 89% of the specimens taken in the clearing series. L. hartmanni dominated the man-biting activity in both habitats. L. trapidoi and L. tintinnabula were distinctly sylvan whereas L. gomezi was taken primarily at the clearing sites. Between-species comparisons of biting activity have been made for both the forest and clearing habitats and are presented in succeeding portions of the results. A list of the phlebotomine sandflies occurring in the Providencia region is presented in Appendix C.

Table II-5

Summary of the common man-biting species taken during the night catches.^a

Species	Forest			Clearing		
	No. of catch periods	No. taken	M_W^b	No. of catch periods	No. taken	M_W
<u>L. hartmanni</u>	987	5422	2.60	432	1361	1.58
<u>L. trapidoi</u>	924	2109	0.91	432	77	0.10
<u>L. yuilli</u>	924	1204	0.54	432	227	0.20
<u>L. panamensis</u>	987	322 ^c	0.13	432	133	0.15
<u>L. tintinnabula</u>	987	141 ^c	0.06	432	2	- ^d
<u>L. bifoliata</u>	987	104 ^c	0.06	432	11	-
<u>L. gomezi</u>	987	95 ^c	0.05	432	384	0.43
<u>W. rotundipennis</u>	987	88	0.05	432	219	0.27
Others ^e		127			23	

^aCatch period 17 excluded.

^b M_W is a modified geometric mean catch per period. See text for definition.

^cThe numbers taken for L. panamensis, L. tintinnabula, L. bifoliata, and L. gomezi are actually somewhat larger for the forest habitat as 57 specimens belonging to these species were not identified.

^d M_W not computed as number taken was very small.

^eIncludes species taken in small numbers and the group of 57 specimens belonging to L. panamensis, L. tintinnabula, L. bifoliata, and L. gomezi.

Vertical Stratification of Man-biting Activity within the Forest

Summary of vertical stratification. The vertical stratification for the entire phlebotomine sandfly population taken in the forest series of man-biting catches is presented in Table II-6. When the catches for the three sites were combined, biting activity in the canopy was greater than at either of the other two levels. The differences between the canopy and the ground and between the canopy and the understory were declared to be statistically highly significant by a nonparametric rank test (Table II-7). However, the pattern of vertical stratification for the entire population varied considerably between the three sites as is evident from Tables II-6 and II-8. Between-site variation of biting activity was greatest in the canopy and least in the understory where the modified geometric mean catch was remarkably similar at all three sites.

The vertical stratifications of man-biting activity for L. hartmanni, L. trapidoi, and L. yuilli are given for each of the forest sites in Tables II-8 and II-9 and are summarized for the three sites combined in Tables II-7 and II-10. When the catches for the three forest sites were considered together, the biting activity of L. hartmanni was detected to be significantly ($P \leq 0.05$) greater in the canopy than at either of the other two levels. However, its pattern of vertical stratification varied between

Table II-6

The vertical stratification of man-biting activity
by all species combined.

Sites	No. of catch periods	No. taken	M_W^a
All Sites			
ground	329	2907	3.6
understory	329	2153	3.3
canopy	329	4962	6.7
Buenos Aires			
ground	119	1846	7.1
understory	119	841	3.4
canopy	119	1731	7.5
Providencia			
ground	103	541	2.5
understory	103	686	3.4
canopy	103	2698	14.1
Tiroteos			
ground	107	520	2.2
understory	107	626	3.3
canopy	107	533	2.6

M_W^a is a modified geometric mean catch per period.
See text for definition.

Table II-7

Comparison of man-biting activity at three levels within the forest by means of a rank test. The three sites are combined.

Species	Total no. of catch periods	Rank totals		Standard error for a difference $(\sqrt{2n})^a$	Standardized difference of rank totals (z)		
		Ground	Under- story		Understory- Ground	Canopy- Ground	Canopy- Understory
All species	329	283.0	247.0	25.30	-1.42	5.81**	7.23**
<u>L. hartmanni</u>	329	299.5	260.5	24.82	-1.57	2.60*	4.17**
<u>L. trapidol</u>	308	126.0	212.5	21.95	3.94**	11.78**	7.84**
<u>L. vuilli</u>	308	162.5	144.0	19.85	-0.93	6.15**	7.08**
<u>L. panamensis</u>	329	76.5	78.5	13.42	0.15	2.87*	2.72*

^aThe n does not correspond with the total number of catch periods because those periods in which all three levels had zero values were omitted.

*p ≤ 0.05

**p ≤ 0.01

Table II-8

Comparison of the vertical stratification of man-biting activity at three forest sites by means of a rank test.

Species	Total no. of catch periods	Rank totals		Standard error for a difference ($\sqrt{2n}$) ^a	Standardized difference of rank totals (z)				
		Ground	Under- story		Canopy	Understory- Ground	Canopy- Ground	Canopy- Understory	
All species									
Buenos Aires 1	119	141.0	60.5	152.5	15.36	-5.24**	0.75	5.99**	
Providencia	103	56.5	67.5	179.0	14.21	0.77	8.62**	7.85**	
Tiroteos	107	85.5	119.0	98.5	14.21	2.36*	0.91	-1.44	
L. hartmanni									
Buenos Aires 1	119	152.5	65.5	133.0	15.30	-5.69**	1.27	4.41**	
Providencia	103	59.0	74.5	157.5	13.93	1.11	7.07**	5.96**	
Tiroteos	107	88.0	120.5	73.5	13.71	2.37*	-1.06	-3.43**	
L. trapidoi									
Buenos Aires 1	106	58.5	57.0	130.5	12.81	-0.12	5.62**	5.74**	
Providencia	95	34.5	58.5	147.0	12.65	1.90	8.89**	7.00**	
Tiroteos	107	33.0	97.0	107.0	12.57	5.09**	5.89**	0.80	
L. yuilli									
Buenos Aires 1	106	72.5	57.0	119.5	12.88	-1.20	3.65**	4.85**	
Providencia	95	36.0	35.5	120.5	11.31	-0.04	7.47**	7.52**	
Tiroteos	107	54.0	51.5	44.5	10.00	-0.25	-0.95	-0.70	
L. gamezi									
Providencia	103	28.0	27.5	88.5	9.80	-0.05	6.17**	6.22**	
W. rotundipennis									
Providencia	103	40.0	35.5	38.5	8.72	-0.52	-0.17	0.34	

^athe n does not correspond with the total number of catch periods because those periods in which all three levels had zero values were omitted.

*p ≤ 0.05

**p ≤ 0.01

Table II-9
Vertical stratification of man-biting activity by site for the common forest species.

Site	<u>L. hartmanni</u>			<u>L. trapidoi</u>			<u>L. yuilli</u>			<u>L. panamensis</u>		
	No. of catch periods	No. taken	M_w^a	No. of catch periods	No. taken	M_w	No. of catch periods	No. taken	M_w	No. of catch periods	No. taken	M_w
Buenos Aires												
ground	119	1329	5.0	106	133	0.7	106	178	0.76	119	17	0.08
understory	119	472	2.0	106	132	0.7	106	122	0.57	119	9	0.05
canopy	119	898	4.2	106	420	1.9	106	269	1.42	119	42	0.15
Providencia												
ground	103	390	1.9	95	35	0.2	95	18	0.10	103	16	0.09
understory	103	465	2.6	95	113	0.6	95	12	0.08	103	32	0.11
canopy	103	1038	5.8	95	897	4.3	95	314	1.73	103	136	0.35
Tiroteos												
ground	107	270	1.3	107	29	0.2	107	145	0.36	107	17	0.09
understory	107	335	1.9	107	150	0.8	107	91	0.31	107	24	0.13
canopy	107	225	1.1	107	200	1.0	107	55	0.25	107	29	0.15

^a M_w is a modified geometric mean catch per period. See text for definition.

Table II-10

Vertical stratification of man-biting activity of the more abundant forest species. The three forest sites are combined.

Species	No. of catch periods	No. taken	M_W^a
<u>L. hartmanni</u>			
ground	329	1989	2.5
understory	329	1272	2.2
canopy	329	2161	3.2
<u>L. trapidoi</u>			
ground	308	197	0.4
understory	308	395	0.7
canopy	308	1517	2.1
<u>L. yuilli</u>			
ground	308	341	0.4
understory	308	225	0.3
canopy	308	638	1.0

M_W^a is a modified geometric mean catch per period.
See text for definition.

the individual sites. The man-biting activity of L. trapi-
doi was greatest in the canopy at all three sites: the
only difference between the canopy and either of the other
two levels that was not declared to be highly significant
was that for the understory at the Tiroteos sites. When
the man-biting catches of L. yuilli for the three forest
sites were combined, biting activity in the canopy was
declared to be significantly greater than either on the
ground or in the understory. At the Buenos Aires and
Providencia sites, its pattern of vertical stratification
was similar to that for the three sites combined, but at
the Tiroteos site a significant difference was not detected
between any of the levels.

If the patterns of vertical stratification of L. hart-
manni, L. trapidoi, and L. yuilli (Table II-8) are compared
by site, differences in vertical stratification related to
the site may be distinguished from those due to the species.
Such comparisons revealed that the patterns of all three
species were similar at the Providencia site but quite
dissimilar at the Tiroteos site. At both the Buenos Aires
and Providencia sites, the biting activity of all three
species was greater in the canopy than in the understory,
and these differences were consistently detected to be
highly significant ($P \leq 0.01$). At the Tiroteos site a
statistically significant difference between the canopy
and the understory was detected only for L. hartmanni, and

in this instance the biting activity was greater in the understory. When the biting activity in the canopy was compared with that on the ground, all three species were declared to have a highly significant preference for the canopy at the Providencia site. With the exception of L. hartmanni, this was also true for the Buenos Aires site. At the Tiroteos site only L. trapidoi was found to have a statistically significant preference for the canopy over the ground level. No significant difference was detected in the magnitudes of biting activity between the understory and ground for any of the species at the Providencia site, and at the Buenos Aires site only L. hartmanni had a statistically significant preference and this was for the ground. At the Tiroteos site the biting activity of L. hartmanni and L. trapidoi was declared to be significantly greater in the understory than at ground level, but no significant difference between these levels was detected for L. yuilli.

The vertical stratifications of man-biting activity of the less frequent forest species are given in Table II-11. The biting activity of L. panamensis for the three sites combined was detected to be significantly ($P \leq 0.05$) greater in the canopy than either in the understory or on the ground. Like the three preceding species, the preference of L. panamensis for the canopy was most pronounced at the Providencia site (Table II-9). However, its

Table II-11

Vertical stratification of man-biting activity of the less frequent forest species. The three forest sites are combined.

Species	No. of catch periods	No. taken	M_W^a
<u>L. panamensis</u>			
ground	329	50	0.09
understory	329	65	0.09
canopy	329	207	0.21
<u>L. tintinnabula</u>			
ground	329	135	0.16
understory	329	4	0.01
canopy	329	2	0.00
<u>L. bifoliata</u>			
ground	329	11	0.02
understory	329	22	0.04
canopy	329	71	0.12
<u>L. gomezi</u> ^b			
ground	103	7	0.04
understory	103	4	0.03
canopy	103	83	0.52
<u>W. rotundipennis</u> ^b			
ground	103	37	0.18
understory	103	21	0.14
canopy	103	26	0.16

^a M_W is a modified geometric mean catch per period.
See text for definition.

^bValues from Providencia forest site only.

preference for the canopy at this site has been exaggerated by an abnormally large catch in the canopy on July 7 of 106 individuals. With only a few exceptions the biting activity of L. tintinnabula was confined to the ground level. A majority of the specimens of L. bifoliata were taken in the canopy. This species' distinct preference for the canopy at the Providencia site was less apparent at the Tiroteos site (Table II-12). The vertical stratifications of man-biting activity observed for L. gomezi and W. rotundipennis are based only on the catches at the Providencia site as they were seldom encountered at the other two forest sites. While L. gomezi was taken primarily in the canopy, a statistically significant preference between levels was not detected for W. rotundipennis.

The vertical stratifications of man-biting activity by those species infrequently encountered are given in Table II-13. The vertical stratifications of diurnal man-biting activity are presented in Table II-14. The little diurnal man-biting activity that did occur was primarily by L. trapidoi in the understory and by L. panamensis on the forest floor. The vertical stratification of males which were occasionally taken during the biting studies is presented in Table II-15.

Table II-12

Vertical stratification of man-biting activity of
L. tintinnabula and L. bifoliata at the
 three forest sites.

Species	No. taken ^a		
	Buenos Aires	Providencia	Tiroteos
<u>L. tintinnabula</u>			
ground	88	3	44
understory	3	0	1
canopy	1	1	0
<u>L. bifoliata</u>			
ground	3	2	7
understory	2	4	16
canopy	5	53	13

^aThe number of catch periods is the same as that given for L. panamensis in Table II-9.

Table II-13

Vertical stratification of man-biting activity of those species infrequently encountered.

	Ground ^a	Understory	Canopy
<u>L. cirrita</u>	7	6	16
<u>L. osornoi</u>	2	1	6
<u>L. serrana</u>	1	2	4
<u>L. verrucarum</u> gr. sp.	- ^b	-	7
<u>L. nocticola</u>	2	-	-
<u>L. olmeca-bicolor</u>	7	-	-
<u>L. shannoni</u>	-	2	5
<u>L. spinosa</u>	-	1	1

^a 329 catch periods per level.

^b A dash indicates that no specimens were encountered.

Table II-14

Vertical stratification of diurnal man-biting activity.

	Ground ^a	Understory	Canopy
<u>L. bifoliata</u>	2	1	- ^b
<u>L. gomezi</u>	1	1	2
<u>L. hartmanni</u>	4	2	1
<u>L. olmeca-bicolor</u>	1	-	-
<u>L. panamensis</u>	10	5	-
<u>L. tintinnabula</u>	-	1	-
<u>L. trapidoi</u>	5	14	1
<u>L. yuilli</u>	1	4	1
<u>W. rotundipennis</u>	-	-	1

^a592 catch periods per level.^bA dash indicates that no specimens were encountered.

Table II-15

Vertical stratification of males encountered on man
during the biting studies.

	Ground ^a	Understory	Canopy
<u>L. hartmanni</u>	65	17	5
<u>L. osornoi</u>	- ^b	1	1
<u>L. trapidoi</u>	-	-	4
<u>L. yuilli</u>	2	-	6

^a 329 catch periods per level.

^b A dash indicates that no specimens were encountered.

Variation in Man-biting Activity
between the Forest Sites

Summary of between-site variation. The total number of Phlebotominae taken at each of the forest sites is given in Table II-16. The modified geometric mean catch for all species combined at the Tiroteos site was only about half as large as those for the other two sites. An analysis of total biting activity during the first seven catch periods indicated that the F ratios for sites, levels, and the sites times levels interaction were all significant at the 1% level (Table II-17). Thus, there is evidence of both a systematic difference in biting activity between the sites regardless of level and of a difference in biting activity between the sites dependent upon level. A statistically significant contrast (Table II-18) between a pair of sites for all levels combined suggests that there is a systematic difference between the two sites over the three levels, although it may also result from the accumulative effect of two contrasts with large values in the same direction. The highly significant ($P \leq 0.01$) Scheffé contrast between the Buenos Aires and Tiroteos sites for the composite population appeared to be due primarily to the relatively large positive contrasts for the ground and canopy. A highly significant interaction in the analysis of variance may be reflected in the Scheffé contrasts. Thus, the contrasts for all levels combined would tend to be statistically not

Table II-16

Total man-biting activity at the three forest sites
for all species combined.

Site	No. of catch periods	No. taken	M_W^a
Buenos Aires	357	4418	5.7
Providencia	309	3925	5.2
Tiroteos	321	1679	2.7

M_W^a is a modified geometric mean catch per period.
See text for definition.

Table II-18
Pairwise contrasts of man-biting activity between three forest sites using Scheffé's
multiple comparison method.

Species	Ground			Understory			Canopy			All levels		
	BA ² vsp	BAvst	Pvst	BAvsp	BAvst	Pvst	BAvsp	BAvst	Pvst	BAvsp	BAvst	Pvst
All species	3.604**	3.223*	-0.269	1.094	0.750	-0.298	-1.104	2.702	3.578**	2.076	3.855**	1.739
<u>L. hartmanni</u>	3.597**	4.140**	0.607	0.951	1.149	0.212	-0.306	2.925*	3.054*	2.447	4.741**	2.236
<u>L. trapidoi</u>	3.393*	3.302*	-0.087	0.893	-0.820	-1.640	-1.422	1.672	2.963*	1.655	2.397	0.711
<u>L. yuillii</u>	3.653**	1.792	-1.782	3.184*	1.684	-1.436	-0.062	5.291**	5.125**	3.912**	5.062**	1.101

²BA = Buenos Aires 1, P = Providencia, T = Tiroteos.

*P ≤ 0.05

**P ≤ 0.01

significant, whereas the corresponding contrasts for the individual levels would tend to be statistically significant in opposite directions. For example, let us consider the contrasts between the Buenos Aires and Providencia sites for the composite population. A significant contrast was not detected for the three levels combined; however, the contrasts of the individual levels varied considerably in magnitude. Thus, while biting activity was significantly greater on the ground at the Buenos Aires site, there is an indication that it was somewhat greater in the canopy at the Providencia site.

The man-biting activity of the common forest species is summarized for each of the forest sites in Table II-19. The modified geometric mean catches of L. hartmanni for the Buenos Aires and Providencia sites were over twice the magnitude of the mean catch at the Tiroteos site. In the analysis of variance for this species, the F ratio for sites was declared to be highly significant, and the sites times levels interaction was statistically significant at the 5% level (Table II-17). The significant difference detected for sites can be primarily attributed to a greater magnitude of biting activity at all three levels at the Buenos Aires site than at the Tiroteos site (Table II-18). The significant interaction is perhaps best reflected in the large variation in the size of the contrasts between the Buenos Aires and Providencia sites. Although the modified

Table II-19

Summary of man-biting activity by species at the
three forest sites.

Site	No. of catch periods	No. taken	M_W^a	No. of catch periods	No. taken	M_W
	<u>L. hartmanni</u>			<u>L. panamensis</u>		
Buenos Aires	357	2699	3.57	357	68	0.09
Providencia	309	1893	3.13	309	184	0.18
Tiroteos	321	830	1.42	321	70	0.12

	<u>L. trapidoi</u>			<u>L. tintinnabula</u>		
Buenos Aires	318	685	1.04	357	92	0.12
Providencia	285	1045	1.16	309	4	0.01
Tiroteos	321	379	0.61	321	45	0.03

	<u>L. yuilli</u>			<u>L. bifoliata</u>		
Buenos Aires	318	569	0.88	357	9	0.02
Providencia	285	344	0.48	309	59	0.10
Tiroteos	321	291	0.30	321	36	0.07

M_W^a is a modified geometric mean catch per period.
See text for definition.

geometric mean catch of L. trapidoi at the Providencia site was nearly twice as large as that at the Tiroteos site, the F ratio for sites was not quite significant at the 5% level. Also, none of the pairwise contrasts for all of the levels combined was declared to be statistically significant. The sites times levels interaction for L. trapidoi was declared to be very highly significant ($P \leq 0.001$) and this is reflected in the pairwise contrasts for the individual levels between the Buenos Aires and Providencia sites and between the Providencia and Tiroteos sites. The geometric mean catch for L. yuilli at the Buenos Aires site was nearly three times as large as that at the Tiroteos site. The F ratios from the analysis of variance for sites, levels, and the interaction were all declared to be very highly significant ($P \leq 0.001$). The two highly significant contrasts for all levels combined reflect the greater amount of biting activity by L. yuilli at the Buenos Aires site than at either of the other sites. The contrasts between the Providencia and Tiroteos sites for the ground and understory are quite similar and differ markedly from the contrast for the canopy.

When the pairwise contrasts in Table II-18 are considered for all three species, some differences in biting activity related to site can be observed. The contrasts for all levels combined suggest that the biting activities of L. hartmanni and L. yuilli were greater at the Buenos

Aires site than at either of the other two sites. Also, for all levels combined, there were no statistically significant differences between the Providencia and Tiroteos sites for any of the three species. This indicates that none of these species had a distinct preference at all three levels for either site. With one exception, the biting activities of all three species at ground level were declared to be significantly greater at the Buenos Aires site than at either of the other two sites. As noted earlier, in the understory the magnitude of biting activity of each species was quite similar at all three sites. In the canopy the biting activities of all three species were declared to be significantly greater at the Providencia site than at the Tiroteos site, but no statistically significant differences were detected between the Providencia and Buenos Aires sites.

The total number of individuals of each of the less abundant species taken in the forest catches is given by site in Tables II-19 and II-20. L. panamensis was taken most frequently at the Providencia site where the modified geometric mean catch was twice as large as that for the Buenos Aires site. L. tintinnabula was most abundant at the Buenos Aires site and was rarely taken in the biting catches at the Providencia site. L. bifoliata was most frequently taken at the Providencia and Tiroteos sites. Man-biting activity by L. gomezi, W. rotundipennis, and L. cirrita was almost entirely confined to the Providencia site.

Table II-20

Distribution by site of the species infrequently taken
during the night forest man-biting catches.

Site:	Buenos Aires	Providencia	Tiroteos
No. of catch periods:	357	309	321
Species			
<u>L. cirrita</u>	- ^a	27	2
<u>L. gomezi</u>	-	94	1
<u>L. nocticola</u>	-	-	2
<u>L. olmeca-bicolor</u>	2	4	1
<u>L. osornoi</u>	-	8	1
<u>L. serrana</u>	-	1	6
<u>L. shannoni</u>	-	4	3
<u>L. spinosa</u>	1	-	1
<u>L. verrucarum</u> group sp.	2	3	2
<u>W. rotundipennis</u>	-	84	4

^aA dash indicates that no specimens were encountered.

Variation in Man-biting Activity
between the Clearing Sites

Abundance comparisons. Total man-biting activity at the six clearing sites for all of the species combined is given in Table II-21. The magnitude of biting activity varied considerably between the sites. Larger numbers were taken at the two forest-clearing margin sites, D and E, than at the sites located within the clearing, i.e., sites A, B, C, and F. The smallest number of specimens was obtained from site A which was adjacent to the Río Anorí and farthest from relatively mature forest.

The man-biting species most frequently taken in the clearing series of catches and the percent of the catch attributed to each are as follows: L. hartmanni, 56%; L. gomezi, 16%; L. yuilli, 9%; W. rotundipennis, 9%; L. panamensis, 5%; and L. trapidoi, 3%. The man-biting activity of these species is summarized for each of the sites in Table II-22. L. hartmanni was the most abundant species at all six of the clearing sites, although L. gomezi was almost as numerous at site C. A highly significant difference in biting activity between the clearing sites was detected for L. hartmanni, L. gomezi, L. yuilli, L. trapidoi, and all species combined (Table II-23). For each of these species and the composite population, a comparison was made by means of a Scheffé contrast between the two forest-clearing margin sites and the four sites within the

Table II-21

Total man-biting activity at the six clearing sites
for all species combined.

Site	No. of catch periods	No. taken	M_W^a
A	72	97	0.8
B	72	259	2.0
C	72	218	1.7
D	72	574	3.9
E	72	821	6.9
F	72	468	2.6

M_W^a is a modified geometric mean catch per period.
See text for definition.

Table II-22

Summary of man-biting activity at the six clearing sites
by the more abundant species.

Site ^a	No. taken	M _W ^b	No. taken	M _W
	<u>L. hartmanni</u>		<u>L. trapidoi</u>	
A	75	0.61	3	0.03
B	186	1.45	2	0.02
C	82	0.72	1	0.01
D	349	2.44	19	0.17
E	439	4.00	36	0.31
F	230	1.50	16	0.11
	<u>L. gomezi</u>		<u>L. yuilli</u>	
A	7	0.07	2	0.02
B	35	0.29	0	0.00
C	80	0.59	13	0.09
D	22	0.17	43	0.32
E	154	1.06	123	0.63
F	86	0.63	46	0.25
	<u>L. panamensis</u>		<u>W. rotundipennis</u>	
A	2	0.02	8	0.06
B	6	0.06	28	0.21
C	7	0.07	33	0.29
D	74	0.41	63	0.43
E	30	0.28	27	0.24
F	14	0.12	60	0.40

^a72 catch periods per site.

^bM_W is a modified geometric mean catch per period.
See text for definition.

Table II-23
Comparisons of man-biting activity between the six clearing sites using Scheffé's multiple comparison method.

Species	F for sites	t ratios for simple differences								Analysis for the contrast D+E vs A+B+C+F		Transformation	
		AVSC ^a	AVSD	AVSE	AVSF	BVSD	BVSF	CVSD	CVSE	DVSE	t ratio		95% confidence interval using Scheffe
All species	8.42**	-b	4.69**	5.66**	3.70*	-	-	-	3.77*	-	5.21**	1.46 to 7.95	$\log_e(x + 1.0)^c$
<u>L. hartmanni</u>	7.35**	-	3.88*	4.57**	-	-	-	3.94*	4.63**	-	5.19**	1.48 to 8.71	$\log_e(x + 1.0)$
<u>L. gomezi</u>	8.98**	4.23*	-	5.44**	4.35**	-	-	-	-	4.44**	0.73		$\log_e(x + 1.0)$
<u>W. rotundipennis</u>	1.66	-	-	-	-	-	-	-	-	-			$\log_e(x + 1.0)$
<u>L. panamensis</u>	1.86	-	-	-	-	-	-	-	-	-			$\log_e(x + 0.1)$
<u>L. yuilli</u>	8.85**	-	-	4.40**	-	4.26*	5.40**	-	3.91*	-	5.41**	2.42 to 84.44	$\log_e(x + 0.1)$
<u>L. trapidoi</u>	5.35**	-	-	-	-	-	-	-	4.07*	-	4.97**	1.97 to 71.24	$\log_e(x + 0.1)$

^aNone of the following single comparisons gave rise to a statistically significant t value and thus have been omitted from the table: A vs B, B vs C, B vs F, C vs F, D vs F, E vs F.

^bA dash indicates a nonsignificant ratio for simple differences.

^cx is the total catch of a species for a given night and site.

*p ≤ 0.05

**p ≤ 0.01

clearing. The comparison for L. gomezi was the only one which was declared to be statistically not significant. The 95% confidence intervals associated with the statistically significant multiple comparisons indicate that the biting activities of L. hartmanni, L. yuilli, L. trapidoi, and the composite population were greater at the two forest margin sites. The confidence intervals for L. yuilli and L. trapidoi are very large, but they do indicate that the biting activities of these two species were, respectively, at least 2.4 and 2.0 times greater at the forest-clearing margin than within the clearing.

When comparisons of biting activity were made between individual sites (Table II-23), statistically significant differences were detected most frequently between sites A and E and between C and E. The pairwise comparisons declared to be statistically significant for L. hartmanni, L. yuilli, and L. trapidoi were always between a forest margin site and one of the sites within the clearing. L. gomezi was the only species for which statistically significant differences were detected between the sites within the clearing, i.e., between A and C and between A and F, and between the two forest-clearing margin sites, D and E. Since a statistically significant difference in biting activity between the six clearing sites was not detected for W. rotundipennis and L. panamensis, the multiple and pairwise comparisons were not computed for

AD-A049 853

WISCONSIN UNIV MADISON DEPT OF VETERINARY SCIENCE
ECOLOGICAL AND AEROSPACE MEDICAL ASPECTS OF VIRUS DISEASES. PAR--ETC(U)
OCT 74 R P HANSON, T M YUILL

F/G 6/3

AFOSR-72-2337

UNCLASSIFIED

AFOSR-TR-75-1645-REV

NL

244

ADA049 853



these species.

For each species in Table II-22 the pattern of its biting activity for the six clearing sites was compared with the pattern of each of the other species and estimates of their similarity are given in Table II-24 as F ratios for interaction between species and sites. The main effect F ratio (F for relative abundance) for each comparison was used as a test of significance for comparing the relative abundance, i.e., as measured by biting activity, of the two species. Statistically significant differences were detected between the pattern of the biting activity of L. gomezi for the clearing sites and the patterns of the other species except for that of W. rotundipennis. When the magnitude of the biting activity of L. gomezi is compared with that of the other species, a significant difference was detected for all of the comparisons except for the one with W. rotundipennis. Thus, the biting activities of L. gomezi and W. rotundipennis at the clearing sites were similar in terms of both the pattern of their biting activity across the six sites and their abundance. The most apparent difference between these two species is in the magnitudes of their biting activity at the two forest-clearing margin sites. A single confidence interval for the abundance ratio was calculated for L. gomezi and W. rotundipennis as the interaction between these two species and sites was not declared to be statistically significant.

Table II-24
Specieswise comparisons of abundance patterns across the six clearing sites.^a

Comparison	F for interaction between species and sites	F for relative abundance ratio	95% confidence interval for abundance ratio	A	B	C	D	E	F
<u>L. hartmanni</u> vs <u>L. gomezi</u>	12.16**	48.96**		3.95-86.60	3.45-10.14	0.61-1.79	10.73-213.79	1.44-13.25	1.33-5.37
<u>L. hartmanni</u> vs <u>M. rotundipennis</u>	3.20*	88.21**		2.03-15.46	2.57-16.08	0.77-4.70	2.10-40.14	5.40-40.83	2.11-6.69
<u>L. hartmanni</u> vs <u>L. panamensis</u>	0.21	140.57**	16.38-52.02						
<u>L. hartmanni</u> vs <u>L. yuillii</u>	4.75**	151.73**		13.58-121.70	80.48-594.70	5.38-135.46	3.32-76.97	2.54-28.57	2.64-74.95
<u>L. hartmanni</u> vs <u>L. trapidoi</u>	2.01	358.83**	29.07-65.26						
<u>L. gomezi</u> vs <u>L. trapidoi</u>	1.19	2.17	0.85-2.69						
<u>M. rotundipennis</u> <u>L. gomezi</u> vs <u>L. panamensis</u>	3.09*	17.91**		0.63-7.64	1.85-21.45	4.70-65.15	0.02-13.51	0.49-55.04	1.88-112.24
<u>L. gomezi</u> vs <u>L. yuillii</u>	11.52**	18.16**		0.63-7.64	11.19-122.31	4.85-137.09	0.05-2.43	0.63-6.03	1.27-21.80
<u>L. gomezi</u> vs <u>L. trapidoi</u>	7.41**	27.62**		0.16-23.63	7.46-37.13	13.39-245.61	0.08-3.67	0.95-14.26	5.38-140.49
<u>M. rotundipennis</u> vs <u>L. panamensis</u>	0.72	5.58*	1.08-2.85						
<u>M. rotundipennis</u> vs <u>L. yuillii</u>	4.04**	9.11**		0.26-20.65	2.89-120.95	2.59-63.53	0.13-4.44	0.07-2.83	0.71-14.44
<u>M. rotundipennis</u> vs <u>L. trapidoi</u>	2.99*	15.69**		0.09-46.85	1.40-50.76	8.22-98.80	0.11-14.81	0.18-3.79	2.54-110.82
<u>L. panamensis</u> vs <u>L. yuillii</u>	1.23	0.02	0.43-2.08						
<u>L. panamensis</u> vs <u>L. trapidoi</u>	0.53	1.42	0.75-2.95						
<u>L. yuillii</u> vs <u>L. trapidoi</u>	1.45	2.31	0.35-1.16						

^aThe transformation $\log_e(x + 1.0)$ was used for L. hartmanni vs M. rotundipennis and M. rotundipennis vs L. panamensis. The transformation $\log_e(x + 0.1)$ was used for all other comparisons. In these transformations x is the total catch of a species for a given night and site. See text for method of transformation selection.

Whenever the F ratio for interaction between sites and the two species is statistically significant, a separate confidence interval is computed for each site. When it is not statistically significant, a single confidence interval is computed. Note that the confidence interval includes 1.0 (ratio 1:1) whenever the main effect F for difference in abundance is not statistically significant.

*p ≤ 0.05

**p ≤ 0.01

Thus, for any one of the six sites, L. gomezi was estimated to be between 0.85 and 2.7 times as abundant as W. rotundipennis. A statistically significant difference between the patterns of biting activity of two species for the clearing sites indicates that the ratios of their biting activity vary significantly between some of the sites. In these instances separate confidence intervals have been constructed for each of the sites. For example, the F ratio for interaction between species and sites for the comparison of L. hartmanni and L. gomezi was declared to be highly significant. Inspection of the confidence intervals for the individual sites reveals a range in the lower limits from 0.6 at site C to 10.7 at site D. A significant difference was not detected between the pattern of biting activity of L. panamensis for the clearing sites and the patterns of any of the other species except L. gomezi. Significant differences were not detected for the comparisons between L. panamensis, L. yuilli, and L. trapidoi for either their patterns of biting activity across the clearing sites or their relative abundances. The relative abundance of L. hartmanni was declared to be highly significantly greater than that of any of the other species.

Diversity and evenness of Phlebotominae man-biting activity. The lowest values of diversity and evenness were associated with the two sites farthest from mature forest, i.e., sites A and B (Table II-25). The estimates

Table II-25

Diversity and evenness of Phlebotominae man-biting
activity at the six clearing sites.

Site	Species diversity ^a H'	Species evenness ^a J'
A	0.86	0.48
B	0.92	0.47
C	1.37	0.70
D	1.28	0.58
E	1.39	0.58
F	1.52	0.69

^aNatural logarithms (\log_e) were employed.

of diversity for the two edge sites, D and E, were slightly less than that for site F at the margin of pioneer vegetation but similar to that for site C within the pasture. The estimates of evenness or equitability for the two edge sites were equal and intermediate between the low values for sites A and B and the higher values for the two most exposed sites, C and F.

Differentiation of Microenvironments and
Species on the Basis of the Man-biting Catches

The first three axes of the ordination of the 132 night catches in eight dimensional species space are presented in Figs. II-8 and II-9. An ordination of the eight species in the space of the catches is given in Fig. II-10. The latter ordination provides a visual means of expressing the degree of similarity between these species as indicated by certain aspects of their man-biting activity. A listing of the raw data for the ordination of the catches is given in Appendix D.

Microenvironment ordination. The ordination of the catches as points in species space will be considered first. Fig. II-8 shows that the first axis separated the catches made in the forest canopy (right end of the axis) from those taken at the sites within the clearing (left end of the axis). The catches for ground level at all three forest sites, for the understory at the Providencia site,

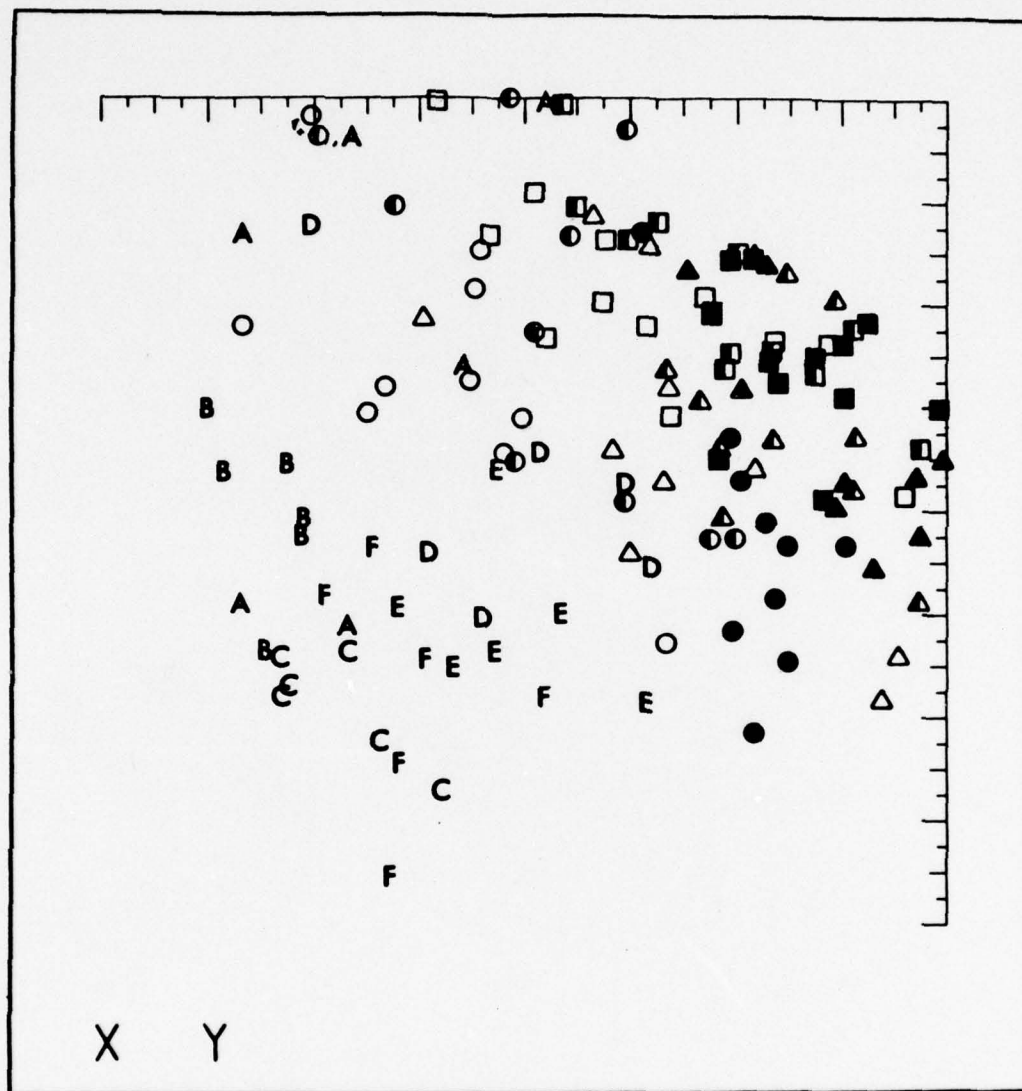


FIGURE II-8

The first two axes of the ordination of the forest and clearing night catches. The first ordination axis is the abscissa and the second is the ordinate. Key to symbols in Figs. II-8 and II-9: A-F = clearing sites, square = Buenos Aires 1 forest site, circle = Providencia forest site, triangle = Tirroteos forest site; open symbols = ground, half open = understory, closed = canopy.

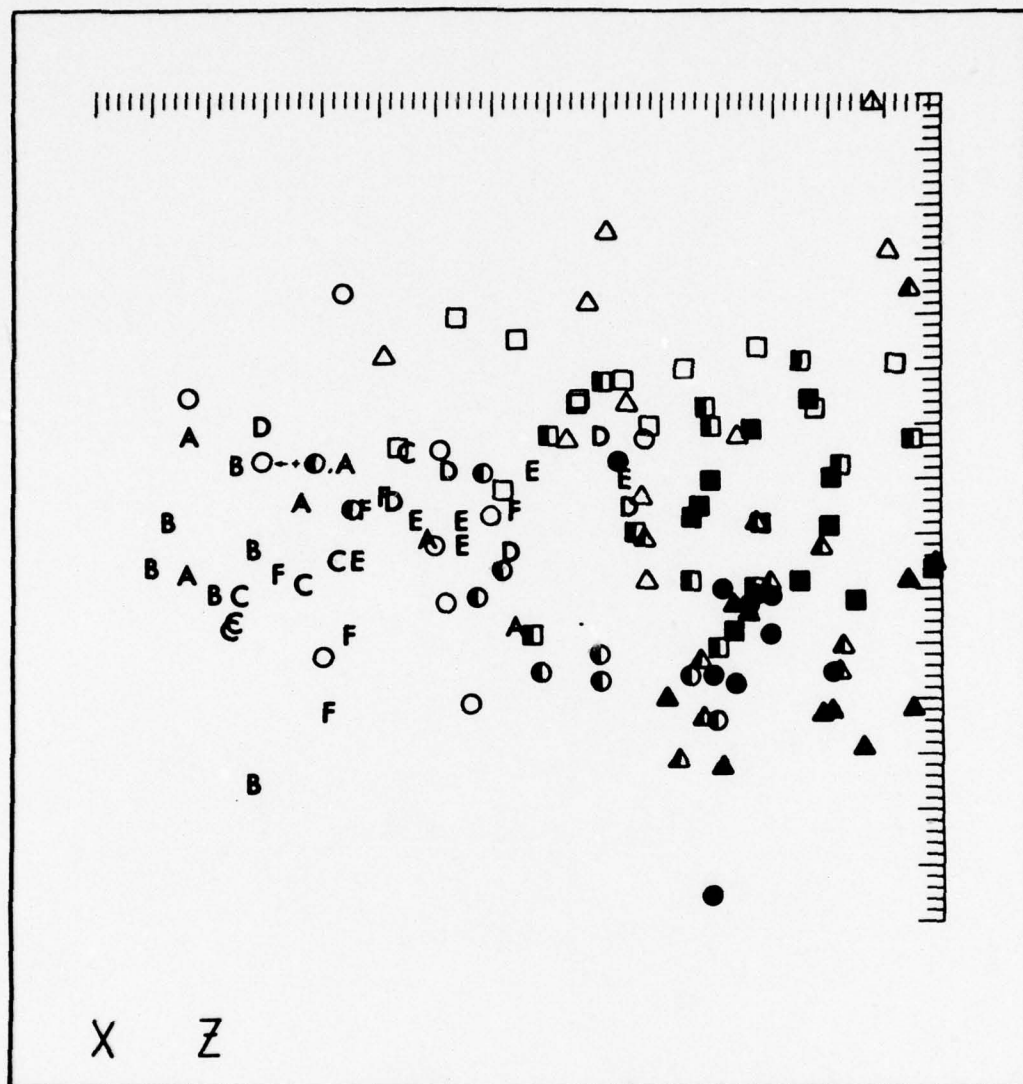


FIGURE II-9

The first and third axes of the ordination of the forest and clearing night catches. The first ordination axis is the abscissa and the third is the ordinate. For key to symbols, see legend to Fig. II-8.

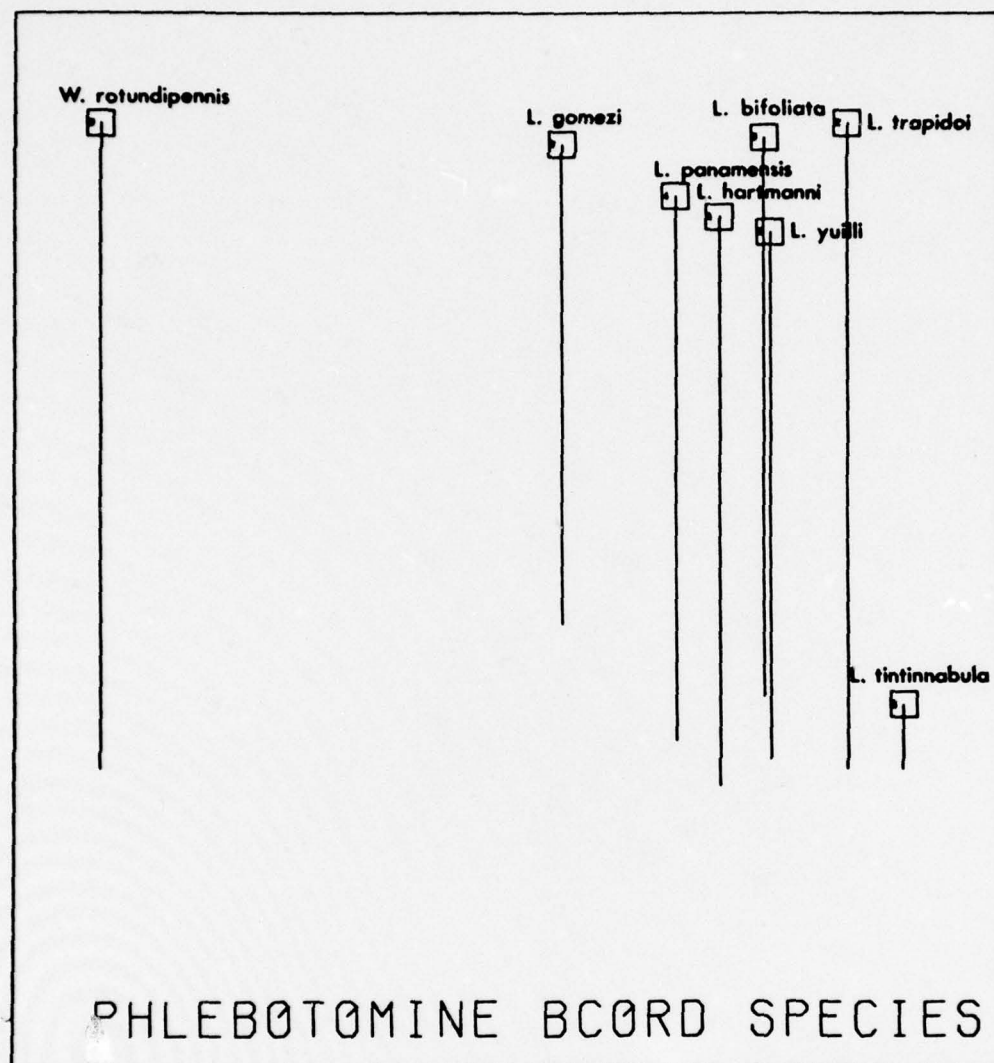


FIGURE II-10

A scatter diagram of the species taken most frequently in the man-biting catches. The species are in the space of the first three ordination axes. The squares may be considered as the heads of pins which are standing on the inclined plane of the first and third ordination axes. The horizontal axis represents the first ordination axis. The length of the pins indicates their position on the second axis.

and for the two edge sites, D and E, tend to be concentrated at the center of the axis. The canopy catches were dominated by L. hartmanni, L. trapidoi, and L. yuilli. The presence of both L. trapidoi and L. yuilli, with one or both occurring in relatively large numbers, and an absence of L. tintinnabula tended to be characteristic of the canopy catches. The biting activity of L. yuilli and/or L. trapidoi was similar in magnitude to that of L. hartmanni in the catches at the extreme right-hand end of the axis. L. panamensis was frequently present in the canopy catches in small numbers. L. hartmanni was ubiquitous, occurring in all 132 of the catches. The catches for clearing sites B, C, and A, which are positioned at the left-hand end of the first axis, were characterized by an absence of L. trapidoi, L. yuilli, L. tintinnabula, and L. bifoliata. Both L. gomezi and W. rotundipennis were nearly always present in these catches, although the latter species usually occurred in small numbers. L. panamensis was present in about half of the catches. Although L. trapidoi and usually L. yuilli were present in the catches near the center of the first axis, they tended to occur at a magnitude much less than that of L. hartmanni.

The second axis (Fig. II-8) has separated many of the ground and understory catches at the Buenos Aires site and understory catches at the Providencia site (upper end of the axis) from the catches for clearing sites C, F, and

E and some of the canopy catches at the Providencia site (lower end of the axis). The understory and ground level catches near the upper end point were dominated by L. hartmanni and rarely contained any other species except L. trapidoi which was also occasionally absent. The catches somewhat below the end point tended to have, in addition, small numbers of L. yuilli and occasionally another species. At the opposite end of this axis, species diversity became considerably greater. L. gomezi, W. rotundipennis, L. panamensis, and L. yuilli were nearly always present and the combined total of these species exceeded that of L. hartmanni.

Together, the first two axes have quite distinctly differentiated the clearing sites B, C, E, and F from the forest sites (Fig. II-8). Clearing sites A and D tend to be more closely associated with the ground and understory catches at the Providencia site and the ground catches at the Tiroteos site. The canopy and understory catches at the Buenos Aires site are clustered in the upper right-hand corner of the ordination and were composed almost exclusively of L. hartmanni, L. trapidoi, and L. yuilli. L. trapidoi tended to be quite numerous in these catches but was somewhat less abundant than L. hartmanni. The canopy catches at the Providencia site are positioned directly below those for the Buenos Aires canopy and understory. The Providencia canopy catches were primarily distinguished

from the latter by having a greater number of species. In addition to the three species taken at the Buenos Aires site, L. gomezi, L. bifoliata, W. rotundipennis, and L. panamensis were present in nearly all of these catches. Many of the forest ground level catches are positioned to the left of the Buenos Aires canopy and understory catches. These ground level catches differed from the latter by having a higher percentage of L. hartmanni relative to L. trapidoi and by the presence of one or two additional species. L. tintinnabula usually occurred in the ground level catches at the Buenos Aires site, and W. rotundipennis was regularly taken on the forest floor at the Providencia site. L. panamensis was present in half of the ground level catches. The catches for clearing sites B, C, E, and F are the furthest away from the Buenos Aires canopy and understory catches and thus are the most dissimilar. W. rotundipennis and L. gomezi were consistently present in these catches, but with the exception of site E, L. trapidoi and L. yuilli were usually absent. L. panamensis was also frequently present. The catches for these clearing sites form groups which partially overlap from site B at the extreme left to site E at the lower center of the ordination.

The third axis, the Z axis in Fig. II-9, positions the ground level catches for the Buenos Aires and Tiroteos sites and a number of Buenos Aires understory catches at

the upper end of the axis and many of the canopy and understory catches for the Tiroteos and Providencia sites at the lower end. The catches near the upper end point tended to have L. yuilli present in larger numbers than L. trapedoi. L. tintinnabula was frequently present and occurred in relatively large numbers in the few instances where L. trapedoi was more abundant than L. yuilli. Although L. bifoliata was absent from the catches at the upper end of the Z axis, it was nearly always present in the catches at the lower end. The catches near the lower end point characteristically had L. trapedoi more abundant than L. yuilli and consistently lacked L. tintinnabula. L. panamensis occurred in a uniform proportion of the catches along the entire length of the Z axis.

Species ordination. The first three axes of the ordination of the eight species as points in the space of the catches is given in Fig. II-10. W. rotundipennis and, to a less extent, L. gomezi are separated from the other species on the first axis. Both of these species were present in nearly all of the clearing catches but, with few exceptions, were taken in the forest catches only at the Providencia site. These two species differed from each other in their biting activity at the two edge sites, D and E, and in their pattern of vertical stratification at the Providencia forest site. Although not considered by the ordination, they also differed in their temporal pattern

of biting activity. The second axis clearly differentiates L. tintinnabula which, unlike the other species, was taken almost exclusively at ground level. L. tintinnabula was encountered primarily at the Buenos Aires and Tiroteos sites and was rarely taken in the clearing catches.

Fig. II-10 suggests that L. panamensis, L. hartmanni, L. yuilli, L. bifoliata, and perhaps L. trapidoi were rather similar in their biting activity; however, some factors such as diel periodicity were not considered in the ordination. Some of the more apparent similarities and differences in the man-biting activity of these five species have already been described in preceding portions of this chapter and form the basis of the following comparisons. The biting activity of each of these species varied in magnitude between the three forest sites (Table II-19). In some instances the between-site differences were detected to be statistically significant (Table II-18). L. hartmanni and L. yuilli had rather similar ratios of biting activity between the three forest sites: both were taken in substantially greater numbers at the Buenos Aires site than at either of the other two locations. L. bifoliata, however, was seldom encountered at the Buenos Aires site and occurred in greatest numbers at the Providencia site. L. trapidoi and L. panamensis were also most numerous at the Providencia site. The total biting activity of each of these five species was greater in the canopy than either

in the understory or on the forest floor. However, the proportion of the catch occurring in the canopy varied considerably between the species and was greatest for L. bifoliata and L. trapidoi. Statistically significant differences were detected between the clearing sites for the man-biting activity of L. hartmanni, L. trapidoi, and L. yuilli. The biting activity of each of these three species was declared to be significantly more abundant at the two edge sites, D and E, than at the sites within the clearing. Although L. panamensis was also taken in greater numbers at the two forest-clearing margin sites than at the sites within the clearing, a statistically significant difference was not detected between these two groups of sites. L. bifoliata was seldom encountered in the clearing catches. The magnitude of biting activity between the forest and clearing habitats was either relatively similar as for L. panamensis and L. hartmanni or decidedly greater at the forest sites. With the exception of L. panamensis, these species did not appear to have large seasonal fluctuations in biting activity.

Neither the habitat nor the species ordinations appear to have been discernibly influenced by seasonality, although this may be due to the relatively small sample size.

Summarization of the Temporal Patterns
of Man-biting Activity in the Forest
and Clearing Habitats

The summary temporal patterns of nocturnal man-biting activity for the entire population and for L. hartmanni, L. trapidoi, L. yuilli, and L. panamensis are presented in Figs. II-11 to II-15 for both the forest and clearing habitats. The number of specimens obtained and the modified geometric mean catch per period are given in Tables II-26 to II-29. The daytime catch periods were not included in the graphs because diurnal biting by phlebotomine sandflies was infrequent (Table II-30) in the Providencia study area.

Within the forest there were extensive variations between nights in the temporal pattern of the man-biting activity of L. hartmanni (Fig. II-16). There were variations in both the time of maximum biting activity and in the shape of the nightly temporal patterns. In Fig. II-17 the nightly temporal patterns presented in Fig. II-16 are partitioned by vertical level. On most of these nights, there tended to be sharp peaks in biting activity at two or all three of the levels. These peaks appeared to be somewhat synchronized, usually occurring within one or two catch periods of each other. There is no indication that the biting activity of L. hartmanni consistently reached a peak earlier at one level than at either of the other two. A summarization by level of the nightly temporal patterns

FIGURE II-11

Summary temporal patterns of man-biting activity in forest and clearing habitats by all species combined based on modified geometric means converted to percentages. Each catch period approximates the corresponding hour as described in the text.

FIGURE II-12

Summary temporal patterns of man-biting activity in forest and clearing habitats by L. hartmanni based on modified geometric means converted to percentages. Each catch period approximates the corresponding hour as described in the text.

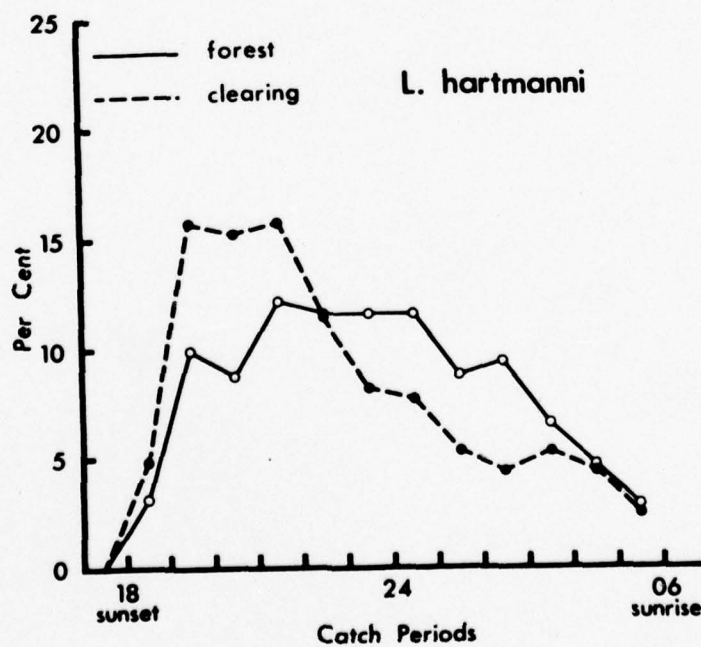
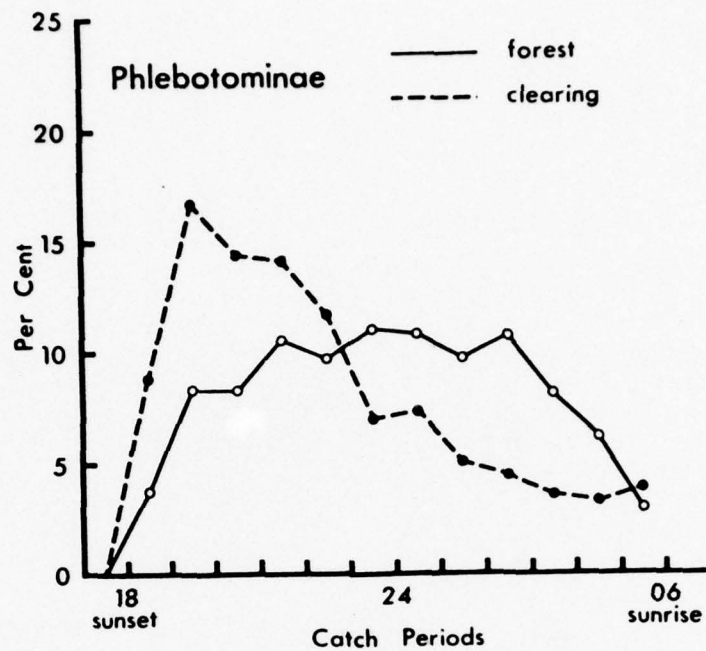
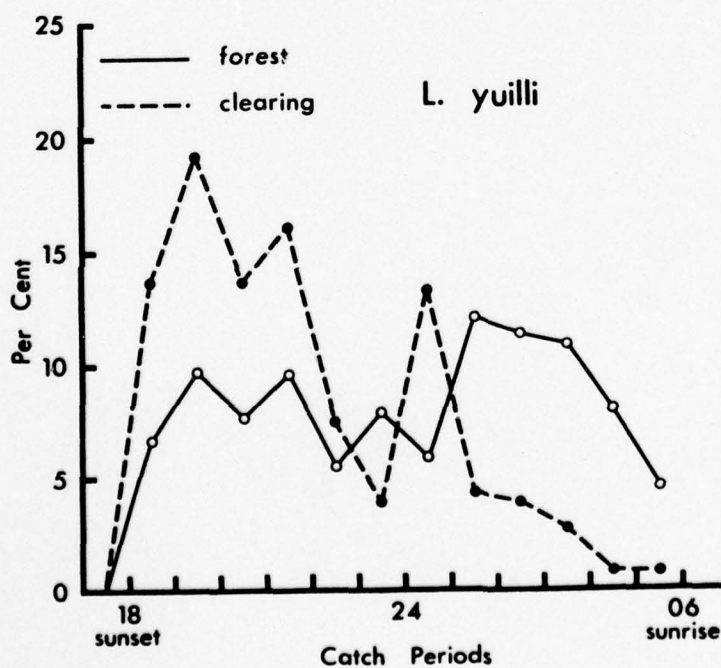
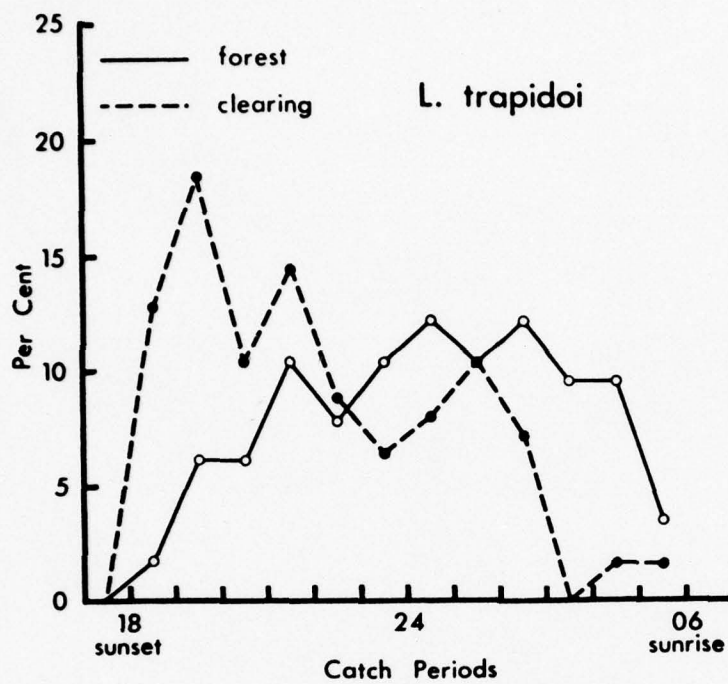


FIGURE II-13

Summary temporal patterns of man-biting activity in forest and clearing habitats by L. trapidoi based on modified geometric means converted to percentages. Each catch period approximates the corresponding hour as described in the text.

FIGURE II-14

Summary temporal patterns of man-biting activity in forest and clearing habitats by L. yuilli based on modified geometric means converted to percentages. Each catch period approximates the corresponding hour as described in the text.



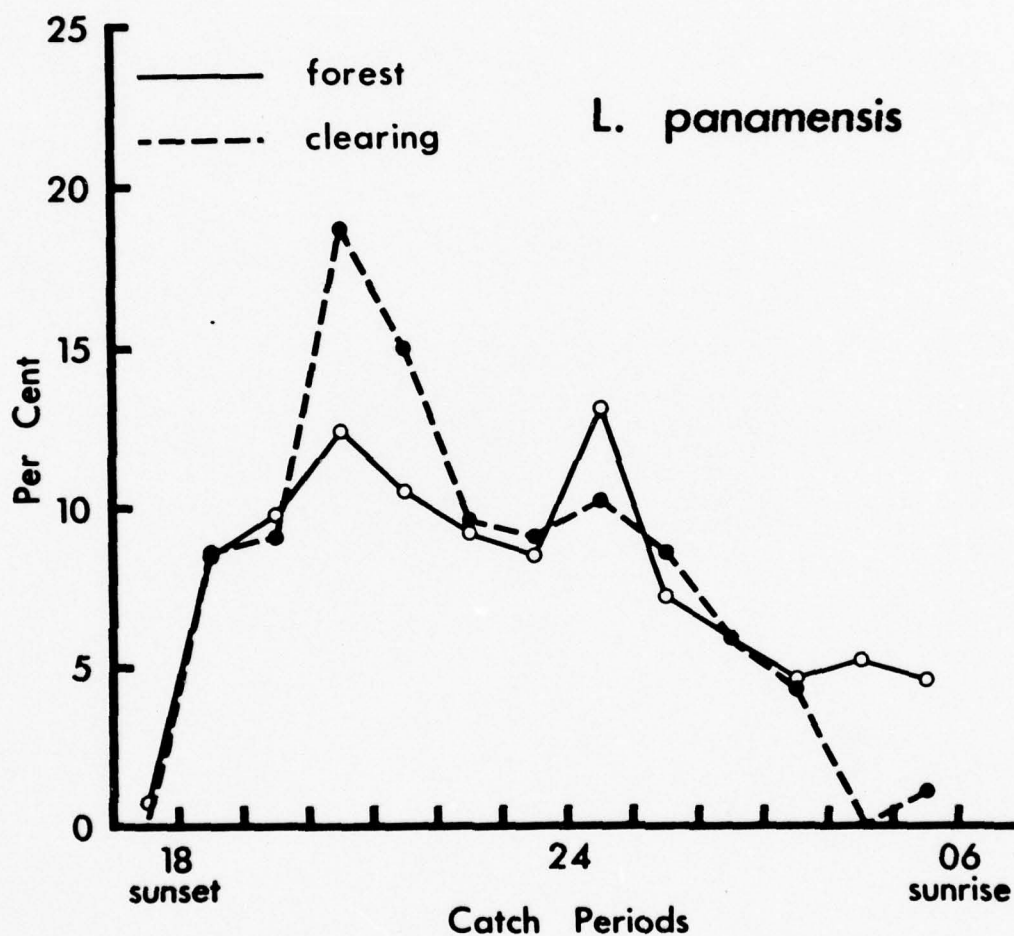


FIGURE II-15

Summary temporal patterns of man-biting activity in forest and clearing habitats by *L. panamensis* based on modified geometric means converted to percentages. Each catch period approximates the corresponding hour as described in the text.

Table II-26

Summary by catch period of all individuals, regardless of species, taken in the night catches for the forest and clearing habitats.

Catch period	Forest			Clearing		
	No. of catch periods	No. taken	M_W^a	No. of catch periods	No. taken	M_W
17	96	8	.1	30	0	.0
18	99	531	2.0	36	220	3.0
19	93	1,159	4.5	36	419	5.7
20	102	1,116	4.5	36	359	4.9
21	96	1,380	5.7	36	343	4.8
22	90	1,064	5.3	36	239	4.0
23	87	953	6.0	36	144	2.4
24	81	893	5.9	36	225	2.5
01	69	791	5.3	36	141	1.7
02	72	723	5.8	36	116	1.5
03	66	655	4.4	36	69	1.2
04	69	506	3.3	36	77	1.1
05	63	250	1.6	36	85	1.3
TOTALS	1,083	10,029	-	462	2,437	-

M_W^a is a modified geometric mean catch per period.
See text for definition.

Table II-27

Summary by catch period of individuals taken in the forest night catches for L. hartmanni, L. panamensis, L. tintinnabula, and L. bifoliata. The three levels are combined.

Catch period	No. of catch periods	<u>L. hartmanni</u>		<u>L. panamensis</u>		<u>L. tintinnabula</u>		<u>L. bifoliata</u>	
		No. taken	M_w^a	No. taken	M_w	No. taken	M_w	No. taken	M_w
17	96	0	0.00	2	0.01	0	0.00	1	0.01
18	99	222	1.05	24	0.13	4	0.03	41	0.20
19	93	719	3.25	38	0.15	17	0.07	19	0.13
20	102	702	2.85	41	0.19	41	0.09	8	0.06
21	96	795	3.88	84	0.16	19	0.10	8	0.05
22	90	658	3.74	31	0.14	25	0.08	5	0.04
23	87	567	3.73	25	0.13	17	0.10	4	0.03
24	81	492	3.70	25	0.20	6	0.05	5	0.04
01	69	328	2.76	13	0.11	4	0.04	0	0.00
02	72	371	2.96	12	0.09	3	0.03	2	0.02
03	66	259	2.14	7	0.07	3	0.03	3	0.03
04	69	206	1.48	12	0.08	2	0.02	1	0.01
05	63	103	0.89	10	0.07	0	0.00	8	0.05
TOTALS		5,422	-	324	-	141	-	105	-

^a M_w is a modified geometric mean catch per period. See text for definition.

Table II-28

Summary by catch period of individuals taken in the forest
night catches for L. trapidoi and L. yuilli.

The three levels are combined.

Catch period	No. of catch periods	<u>L. trapidoi</u>		<u>L. yuilli</u>	
		No. taken	M_W^a	No. taken	M_W
17	87	3	0.02	0	0.00
18	90	49	0.24	87	0.44
19	84	119	0.71	134	0.64
20	93	137	0.73	104	0.51
21	87	213	1.16	116	0.63
22	81	190	0.90	76	0.36
23	78	199	1.19	86	0.52
24	78	251	1.42	65	0.39
01	66	220	1.15	197	0.80
02	72	231	1.39	92	0.75
03	66	232	1.13	130	0.72
04	69	206	1.08	66	0.53
05	60	62	0.37	51	0.30
TOTALS		2,112	-	1,204	-

M_W^a is a modified geometric mean catch per period.
See text for definition.

Table II-29
Summary by catch period of individuals taken in the clearing night catches
for the more abundant species.

Catch period	No. of catch periods	<u>L. hartmanni</u>		<u>L. trapidoi</u>		<u>L. yuilli</u>		<u>L. panamensis</u>		<u>L. gomezi</u>		<u>L. rotundipennis</u>	
		No. taken	M_W^a	No. taken	M_W	No. taken	M_W	No. taken	M_W	No. taken	M_W	No. taken	M_W
17	30	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
18	36	61	1.05	8	0.16	28	0.35	9	0.16	96	1.47	9	0.17
19	36	216	3.25	20	0.23	50	0.49	16	0.17	73	0.94	31	0.43
20	36	206	3.17	7	0.13	41	0.35	31	0.35	36	0.57	35	0.48
21	36	206	3.28	12	0.18	32	0.41	27	0.28	24	0.44	41	0.70
22	36	137	2.40	6	0.11	13	0.19	9	0.18	23	0.38	51	0.73
23	36	96	1.66	4	0.08	6	0.10	9	0.17	10	0.15	15	0.28
24	36	128	1.64	6	0.10	37	0.34	11	0.19	29	0.29	11	0.16
01	36	88	1.08	7	0.13	7	0.11	9	0.16	20	0.31	9	0.16
02	36	72	0.89	5	0.09	7	0.10	7	0.11	17	0.27	7	0.13
03	36	56	1.07	0	0.00	4	0.07	4	0.08	3	0.06	2	0.04
04	36	63	0.93	1	0.02	1	0.02	0	0.00	6	0.10	6	0.11
05	36	32	0.46	1	0.02	1	0.02	1	0.02	47	0.69	2	0.04
TOTALS		1,361	-	77	-	227	-	133	-	384	-	219	-

M_W^a is a modified geometric mean catch per period. See text for definition.

Table II-30

The temporal distribution of diurnal man-biting activity
within the forest for each species
taken in the daytime catches.^a

Catch period	No. of catch periods	<u>L. bifoliata</u>	<u>L. gomezi</u>	<u>L. hartmanni</u>	<u>L. olmeca-bicolor</u>	<u>L. trapidoi</u>	<u>L. yuilli</u>	<u>L. panamensis</u>	<u>L. tintinnabula</u>
07	156	1	1	2	- ^b	1	4	3	-
08	168	1	-	1	-	2	-	1	-
09	174	-	1	2	1	3	-	1	-
10	174	-	-	2	-	-	1	2	1
11	174	-	2	-	-	2	-	2	-
12	171	-	-	-	-	-	-	-	-
13	171	-	-	-	-	-	1	1	-
14	171	-	-	-	-	4	-	-	-
15	171	-	-	-	-	3	-	2	-
16	150	-	-	-	-	2	-	1	-
TOTALS		2	4	7	1	17	6	13	1

^a Summarized over sites and vertical levels. The diurnal catch period 17 is included in Tables II-27 and II-28 with the nocturnal catch periods.

^b A dash indicates that no specimens were encountered.

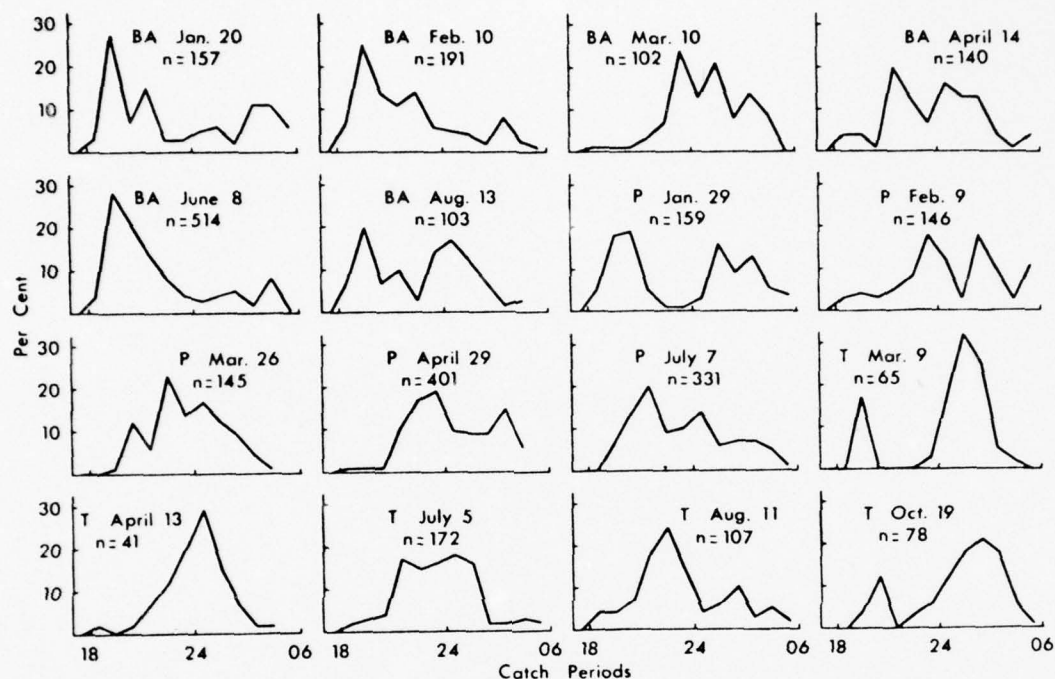
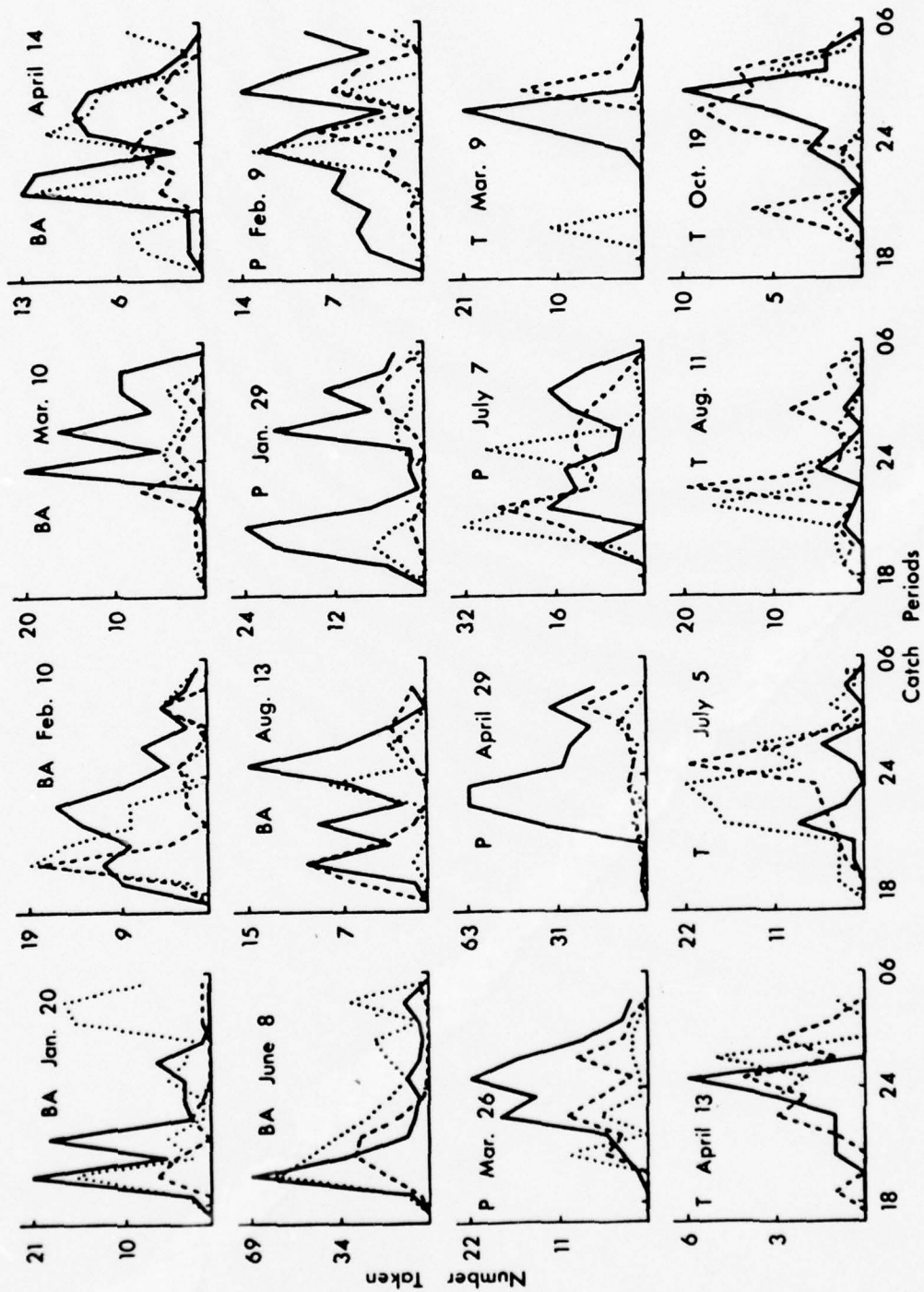


FIGURE II-16

Variation between nights in the temporal pattern of the man-biting activity of *L. hartmanni* for selected forest catches. Key to symbols: BA = Buenos Aires 1 platform site, P = Providencia platform site, T = Tiroteos platform site, and n = the total number of individuals of this species taken throughout the night for all three vertical levels combined. All dates are for 1971.

FIGURE II-17

Nightly temporal patterns of the man-biting activity of L. hartmanni partitioned by vertical level. The scales have been adjusted so that the greatest ordinate in each graph is of the same height. Key to symbols: the solid, dashed, and dotted lines represent biting activity at the canopy, understory, and ground levels, respectively; BA = Buenos Aires I platform site, P = Providencia platform site, and T = Tiroteos platform site. All dates are for 1971.



of the biting activity of L. hartmanni is not presented since an averaging of such highly variable biting activity would tend to distort its true nature.

There was also a considerable amount of between-night variation in the temporal biting pattern of L. hartmanni for the clearing catches (Fig. II-18). The extent of between-night differences in the temporal biting pattern at each clearing site appeared to be partially related to the site, e.g., the temporal pattern at site E was quite variable while at site D it was relatively uniform (Fig. II-18). Most of the catches at sites A, B, C, and F contained an insufficient number of individuals to be meaningfully graphed. The modified geometric mean catches for periods 18 through 21 were similar between the forest and clearing habitats but became substantially reduced in the latter after 2100 hours.

The biting activity of L. trapidoi also tended to be concentrated earlier in the clearing than in the forest habitat (Fig. II-13). However, the modified geometric mean of each catch period was consistently larger for the forest than the clearing habitat. The biting activity of L. trapidoi at the clearing sites occurred at such a low magnitude (Table II-5) that further meaningful observations concerning the temporal pattern of its biting activity in this habitat cannot be made. Fig. II-19 indicates that within the forest there was considerable variation between nights in the

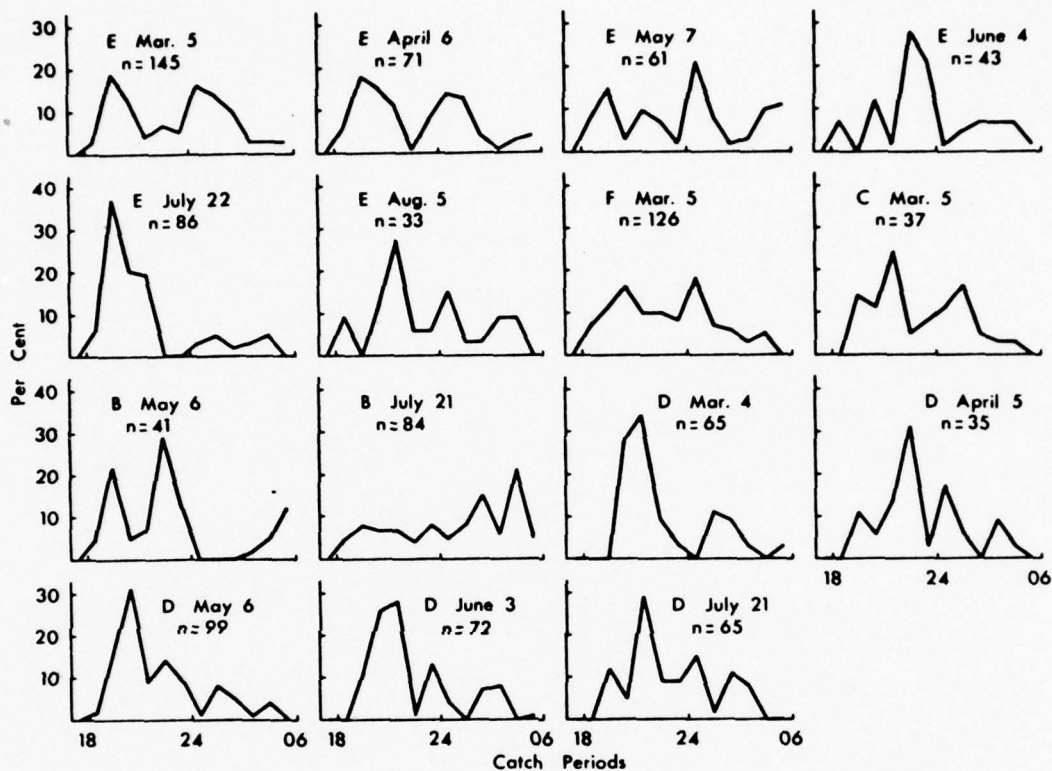


FIGURE II-18

Variation between nights in the temporal pattern of the man-biting activity of *L. hartmanni* for selected clearing catches. Key to symbols: A to F = the six clearing sites and n = the total number of individuals of this species taken throughout the night. All dates are for 1971.

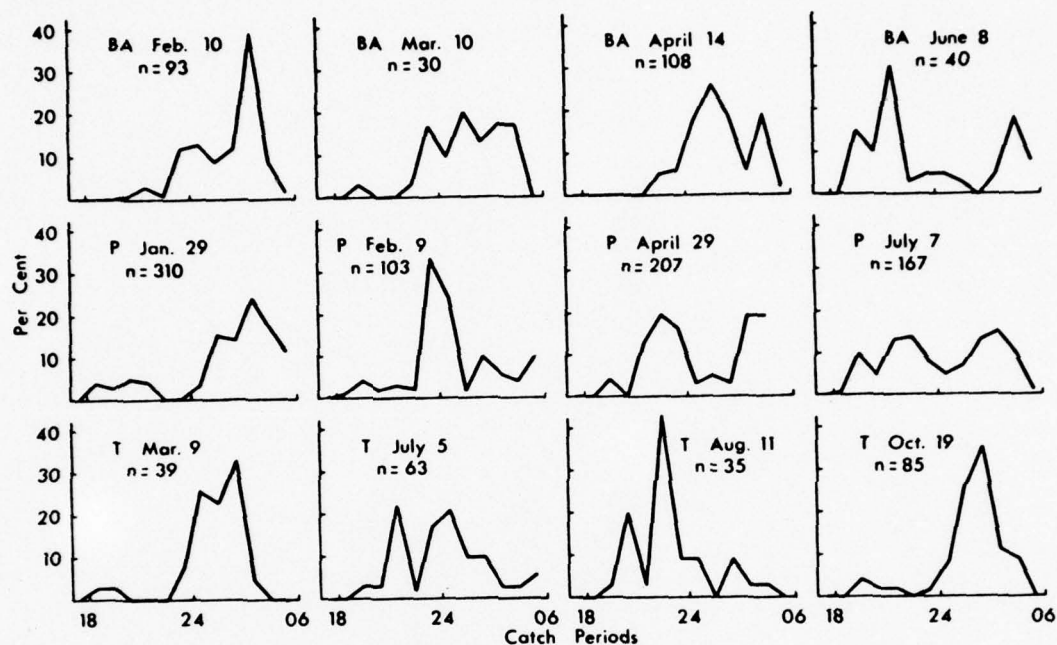


FIGURE II-19

Variation between nights in the temporal pattern of the man-biting activity of *L. trapidoi* for selected forest catches. Key to symbols: BA = Buenos Aires 1 platform site, P = Providencia platform site, T = Tiroteos platform site, and n = the total number of individuals of this species taken throughout the night for all three vertical levels combined. All dates are for 1971.

temporal pattern of biting activity and that prominent peaks in biting activity occurred on a number of the nights. Figs. II-13 and II-20 thus present a distortion of the nightly temporal patterns of biting activity which were frequently in the form of a transient wave. However, Table II-31 and Fig. II-20 do indicate that the biting activity of L. trapidoi at the ground and understory levels was not concentrated in a limited portion of the night. An examination of the catches for individual nights indicated that there frequently was some synchronization of biting activity between the three vertical levels; however, there was no evidence that the biting activity of this species tended to reach a peak at one level before reaching a peak at another. Fig. II-20 also reveals that very little biting activity occurred at ground level during the first three catch periods after sunset. Although sample size was insufficient to determine the extent of between-site variation in the temporal patterns of biting activity, no striking differences were apparent.

The man-biting activity of L. yuilli tended to be concentrated somewhat earlier in the clearing than in the forest habitat (Fig. II-14). As with L. trapidoi, the modified geometric mean of each catch period was larger for the forest than the clearing habitat (Tables II-28 and II-29). Again, the summary temporal patterns (Fig. II-14) distorted the nature of the nightly biting activity. The

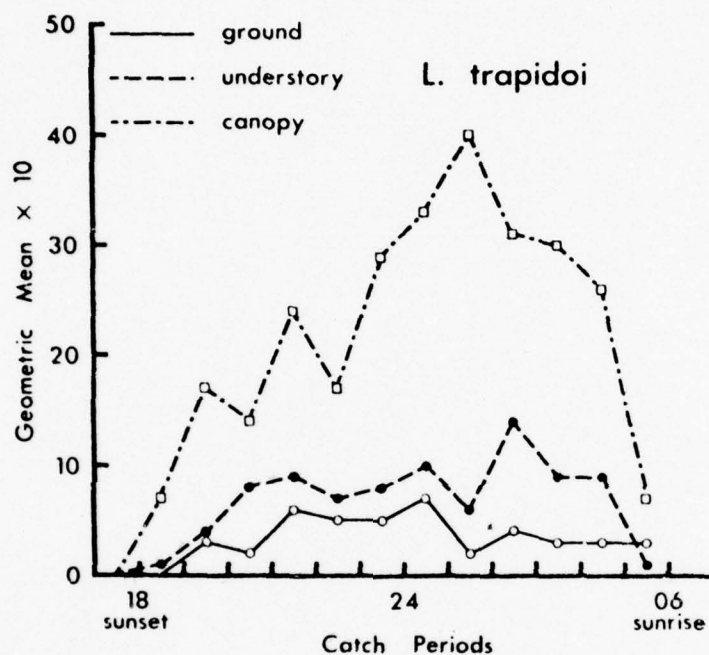


FIGURE II-20

Summary temporal patterns of man-biting activity at three levels within the forest for *L. trapidoi* based on modified geometric means. Each catch period approximates the corresponding hour as described in the text.

Table II-31

Summary of individuals taken in the forest night catches by vertical level and catch period for L. trapidoi.

Catch period	No. of catch periods	Ground level		Understory		Canopy	
		No. taken	M_W^a	No. taken	M_W	No. taken	M_W
17	29	2	0.04	1	0.02	0	0.00
18	30	1	0.02	5	0.12	43	0.66
19	28	18	0.32	20	0.43	81	1.68
20	31	12	0.20	43	0.83	82	1.39
21	29	31	0.57	52	0.89	130	2.41
22	27	25	0.51	38	0.69	127	1.70
23	26	25	0.54	36	0.77	138	2.88
24	26	34	0.66	51	0.98	166	3.30
01	22	7	0.21	20	0.63	193	4.02
02	24	14	0.41	56	1.37	161	3.06
03	22	10	0.29	35	0.88	187	2.99
04	23	11	0.32	36	0.89	159	2.63
05	20	9	0.33	3	0.11	50	0.73
TOTALS		199	-	396	-	1,517	-

M_W^a is a modified geometric mean catch per period.
See text for definition.

temporal pattern of the man-biting activity of L. yuilli was quite variable from one night to another (Fig. II-21) and often there was a sudden, pronounced surge in biting activity lasting for only one or two catch periods. An extreme example occurred on April 13 at the Tiroteos site where over one half of the individuals taken there at ground level were captured during a single catch period. A nightly pattern of vertical movement was not apparent from the biting catches. On many of the nights there appeared to be a synchronization of biting activity at the three vertical levels. An insufficient number of catches were made at the three forest sites to determine between-site differences in the temporal patterns of biting activity. However, the biting activity of L. yuilli during the first catch period after sunset tended to be relatively high at the Buenos Aires and Providencia sites but was very reduced at the Tiroteos site.

The summary temporal patterns of the man-biting activity of L. panamensis for the forest and clearing habitats were rather similar (Fig. II-15). This was also true of the modified geometric means of each catch period (Tables II-27 and II-29); however, the means for catch periods 20 and 21 were noticeably greater for the clearing than the forest. Another apparent difference was that only one individual of L. panamensis was taken during the last two catch periods in the clearing. Biting activity within the

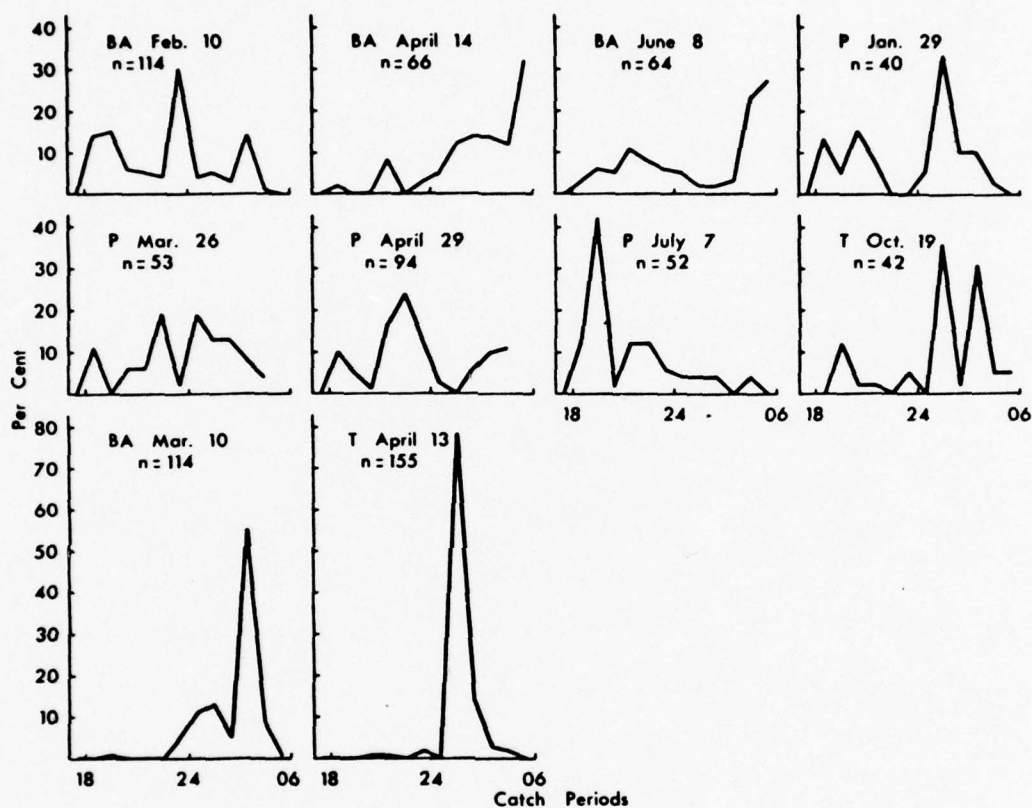


FIGURE II-21

Variation between nights in the temporal pattern of the man-biting activity of *L. yuilli* for selected forest catches. Key to symbols: BA = Buenos Aires 1 platform site, P = Providencia platform site, T = Tiroteos platform site, and n = the total number of individuals of this species taken throughout the night for all three vertical levels combined. All dates are for 1971.

forest tended to be rather sporadic during the night, and there was no good evidence of a synchronization of biting activity over the three vertical levels. Thus, Fig. II-15 provides only an indication of when biting is most likely to occur during the night.

L. tintinnabula was not abundant in the man-biting catches. Its biting activity occurred primarily at ground level and at the Buenos Aires site. Although this species was taken in most of the night catches at the Buenos Aires site, its biting activity was sporadic throughout the night. When summarized over all of the catch nights, the biting activity of L. tintinnabula was concentrated between about 1900 hours and midnight (Fig. II-22).

The man-biting activity of L. bifoliata at the forest sites was distinctly concentrated in the first two catch periods after sunset (Fig. II-23).

The summary temporal patterns of man-biting activity for L. gomezi and W. rotundipennis in the clearing are presented in Figs. II-24 and II-25. There was a distinct peak in the biting activity of L. gomezi during the first two catch periods after sunset. A second, smaller peak occurred in the catch period preceding sunrise. In April, a collection was made at each of the six clearing sites for the first catch period after sunrise. A total of 15 phlebotomine sandflies were obtained, 13 of which were L. gomezi. Phlebotominae were rarely taken in the series of daytime

FIGURE II-22

Summary temporal pattern of man-biting activity in the forest by L. tintinnabula based on modified geometric means converted to percentages. Each catch period approximates the corresponding hour as described in the text.

FIGURE II-23

Summary temporal pattern of man-biting activity in the forest by L. bifoliata based on modified geometric means converted to percentages. Each catch period approximates the corresponding hour as described in the text.

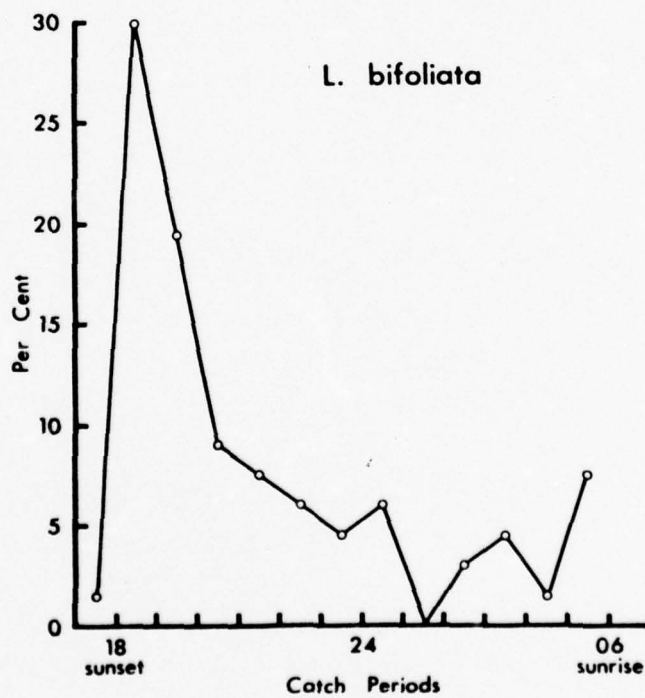
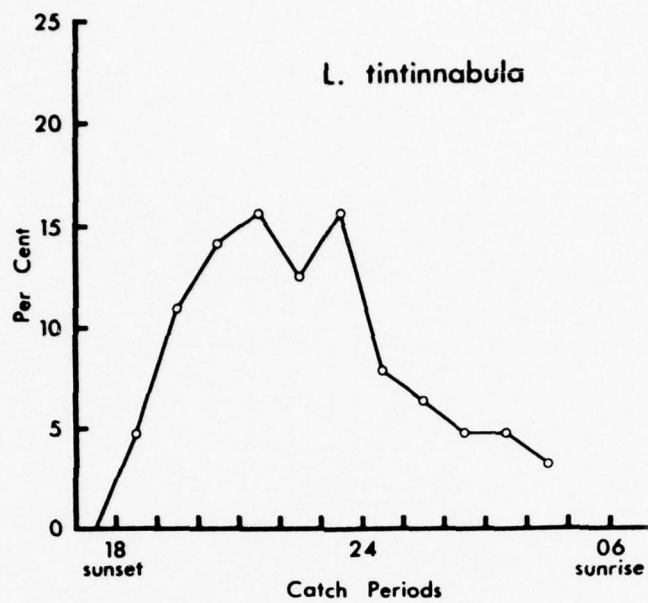
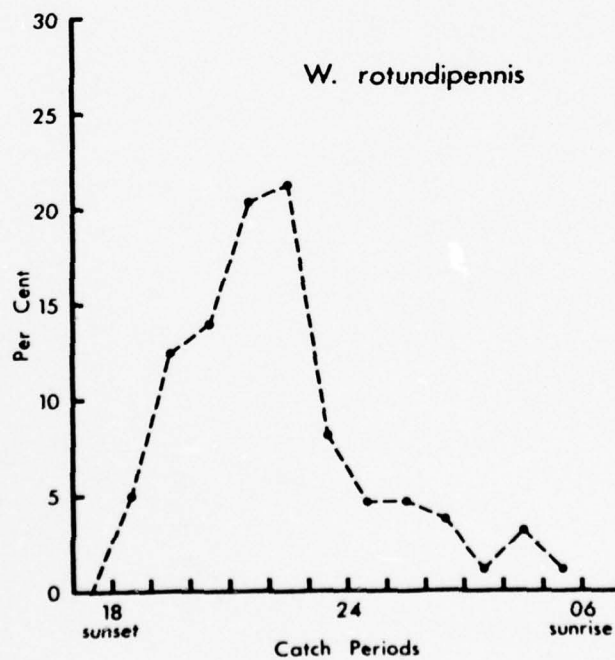
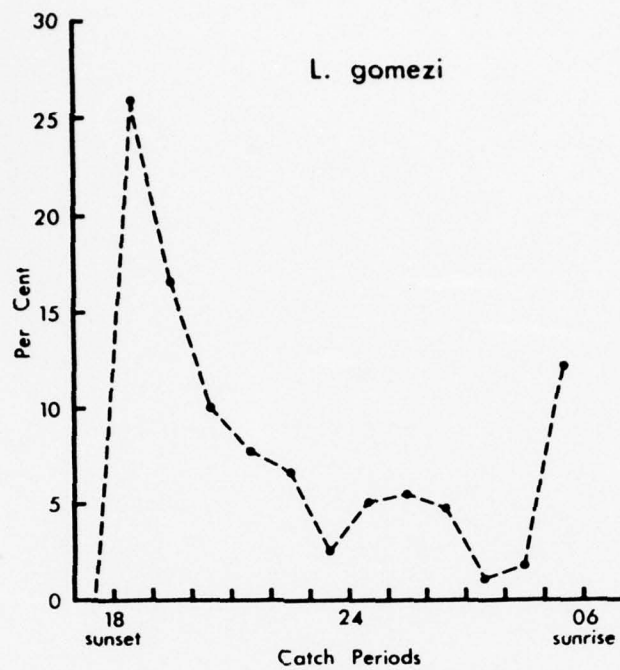


FIGURE II-24

Summary temporal pattern of man-biting activity at the clearing sites by L. gomezi based on modified geometric means converted to percentages. Each catch period approximates the corresponding hour as described in the text.

FIGURE II-25

Summary temporal pattern of man-biting activity at the clearing sites by W. rotundipennis based on modified geometric means converted to percentages. Each catch period approximates the corresponding hour as described in the text.



catches in the clearing, indicating that L. gomezi was not active after 0700 hours. The biting activity of W. rotundipennis in the clearing occurred primarily before midnight (Fig. II-25). L. gomezi and W. rotundipennis occurred in relatively small numbers in the forest series of catches and the temporal distribution of specimens taken is presented in Table II-32. Although the biting activity of L. gomezi tended to be of slightly greater frequency during the first catch period after sunset, there was no distinct concentration of biting activity such as occurred in the clearing. The temporal distributions of other species infrequently taken during the forest and clearing catches are presented in Tables II-32 and II-33. The temporal distribution of males occasionally encountered on man during the biting studies is given in Table II-34.

Seasonality of Man-biting Activity

Since only three, and in some instances two, night forest catches were made per month, the seasonal patterns presented in Table II-35 are crude. With the exception of L. traidoi and L. yuilli, the values in Table II-35 for July include a catch at the Buenos Aires site for both 1970 and 1971 and the values for August include a catch at both the Buenos Aires and Providencia sites for these two years. The catches for September through December were made entirely in 1970 while those for January through June were made

Table II-32

Temporal distribution of man-biting activity of those species infrequently taken in the forest night catches.

Catch period	No. of catch periods	<u>W. rotundipennis</u>	<u>L. gomezi</u>	<u>L. cirrita</u>	<u>L. osornoi</u>	<u>L. serrana</u>	<u>L. verrucarum</u> group sp.	<u>L. nocticola</u>	<u>L. olmea-bicolor</u>	<u>L. shannoni</u>	<u>L. spinosa</u>
17	96	1	^a	-	-	-	-	-	1	-	-
18	99	-	13	-	1	3	1	-	2	-	-
19	93	1	6	9	3	1	3	-	-	3	-
20	102	6	5	9	-	1	1	-	-	1	1
21	96	6	12	5	2	-	-	1	1	-	-
22	90	9	7	2	1	-	-	-	-	2	-
23	87	14	9	-	-	1	1	-	1	-	-
24	81	19	9	1	-	1	-	-	1	-	-
01	69	8	9	2	1	-	-	-	-	1	-
02	72	6	2	1	-	-	-	-	1	-	-
03	66	10	8	-	1	-	1	-	-	-	1
04	69	3	7	-	-	-	-	1	-	-	-
05	63	6	8	-	-	-	-	-	-	-	-
TOTALS		89	95	29	9	7	7	2	7	7	2

^aA dash indicates that no specimens were encountered.

Table II-33
Temporal distribution of man-biting activity of those species infrequently
taken in the clearing night catches.^a

Catch period	No. of catch periods	<u>L. bifoliata</u>	<u>L. osornoi</u>	<u>L. tintinnabula</u>	<u>L. verrucarum</u> group sp.
17	30	^b -	-	-	1
18	36	6	2	-	-
19	36	2	8	-	1
20	36	1	1	-	1
21	36	-	-	-	1
22	36	-	-	-	-
23	36	-	2	-	1
24	36	1	1	1	-
01	36	1	-	-	-
02	36	-	-	-	1
03	36	-	-	-	-
04	36	-	-	-	-
05	36	-	-	1	-
TOTALS		11	14	2	6

^aOne specimen of L. cirrita, L. pessoana, and L. olmea-bicolor was also taken.

^bA dash indicates that no specimens were encountered.

Table II-34

Temporal distribution of male sandflies encountered on man during the biting studies.

Catch period	No. of catch periods	Forest				Clearing ^a		
		<u>L. hartmanni</u>	<u>L. osornoi</u>	<u>L. trapidoi</u>	<u>L. yuillii</u>	<u>L. hartmanni</u>	<u>L. osornoi</u>	
		L.	L.	L.	L.	L.	L.	
17	96	- ^b	-	-	-	30	-	-
18	99	41	1	-	-	36	6	18
19	93	21	1	-	-	36	7	-
20	102	4	-	-	-	36	4	1
21	96	7	-	-	2	36	1	-
22	90	-	-	-	1	36	1	-
23	87	3	-	-	-	36	-	-
24	81	2	-	-	2	36	-	-
01	69	1	-	-	-	36	1	-
02	72	5	-	-	1	36	2	-
03	66	-	-	2	-	36	-	-
04	69	2	-	1	2	36	-	-
05	63	1	-	1	-	36	-	-
TOTALS		87	2	4	8		22	19

^aOne male of L. cirrita was also taken.

^bA dash indicates that no specimens were encountered.

Table II-35

Summary by month of individuals taken in the forest night catches for all species combined and the more abundant species.

Month:	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
No. of catch periods:	99	102	105	102	81	78	102 ^a	126 ^b	36	48	51	57
<u>All species</u>												
No. taken	836	885	733	1328	832	835	1525	855	481	706	377	629
M_W^c	3.65	5.06	2.59	5.18	5.68	4.86	6.44	2.55	6.87	5.28	3.57	5.26
<u>L. hartmanni</u>												
No. taken	375	429	322	582	507	620	703	498	353	374	243	416
M_W	2.19	2.48	1.34	2.50	3.61	3.38	3.47	2.08	5.59	2.66	2.10	3.37
<u>L. panamensis</u>												
No. taken	8	10	13	11	22	58	162	15	5	7	3	8
M_W	0.05	0.07	0.07	0.07	0.13	0.35	0.46	0.07	0.08	0.10	0.04	0.09
<u>L. trapidoi</u>												
No. taken	354	232	186	332	161	63	235	70	72	191	58	155
M_W	0.86	1.07	0.64	0.97	1.06	0.50	1.45	0.45	0.89	1.65	0.72	1.34
<u>L. yuilli</u>												
No. taken	59	181	174	315	81	69	69	29	33	110	58	26
M_W	0.28	0.89	0.70	0.99	0.38	0.49	0.34	0.20	0.46	1.04	0.61	0.28

^aThe number of catch periods for L. trapidoi and L. yuilli is 84.

^bThe number of catch periods for L. trapidoi and L. yuilli is 81.

^c M_W is a modified geometric mean catch per period. See text for definition.

entirely in 1971. In September and December a catch was not made at the Tiroteos site and in October and November a catch was not made at the Providencia site.

The seasonal pattern of man-biting activity for all of the species combined was relatively uniform and did not decrease appreciably during the December through March dry season, although the rainfall for this period was abnormally high. The seasonal pattern of the biting activity of L. hartmanni resembled that of the composite population. The seasonal pattern of L. trapidoi was rather erratic but did not have a noticeable decline during the dry season. L. panamensis had the most distinctive seasonal pattern with a definite peak occurring in June and July. During the six-month period from March to August in which the series of clearing night catches were made, L. panamensis was most numerous in the June catches while all of the other common species were most abundant in the March catches.

Species Using the Base of Trees
as a Diurnal Resting Site

A summary of the phlebotomine sandflies collected from the base of 11 trees over an eight-month period is given in Table II-36. L. trinidadensis (Newstead) and L. bifoliata were the most abundant species, accounting for 47% and 22%, respectively, of the specimens taken. A consider-

Table II-36

Summary of phlebotomine sandflies aspirated from the base of 11 trees
over an eight-month period.

Tree:	1	2	3	4	5	6	7	8	9	10	11	
No. of collections:	7	7	8	7	7	8	7	7	4	7	6	
Species	Sex											Totals
<u>L. trinidadensis</u>	M 39	34	21	36	26	118	42	30	8	39	26	419
	F 4	16	10	11	13	61	33	21	7	13	48	237
<u>L. bifoliata</u>	M 6	17	- ^a	-	-	167	7	5	21	4	1	228
	F 6	8	3	-	-	43	3	3	11	2	1	80
<u>L. abannonci</u>	M 2	17	6	5	6	36	6	14	4	2	5	103
<u>L. shannoni</u>	M 5	10	4	-	7	59	14	14	11	4	1	129
<u>L. abannonci-shannoni</u> ^b	F 1	8	11	5	7	25	3	9	2	3	3	77
<u>L. spinosa</u>	M 2	3	1	3	-	15	4	13	1	6	2	50
	F -	-	-	-	-	5	2	2	1	-	3	13
<u>L. vespertilionis</u>	M 5	1	3	1	8	4	1	3	2	-	2	30
	F 1	-	-	-	3	-	-	-	-	-	-	4
<u>L. tuberculata</u>	F 1	1	-	-	-	-	-	1	-	-	-	3
<u>L. osborni</u>	M 1	-	-	-	-	-	-	1	-	-	-	2
<u>L. pilosa</u>	M -	1	-	-	-	-	-	-	-	-	-	1
	F -	-	-	-	-	1	-	-	-	-	-	1
<u>L. triramula</u>	M -	-	-	-	1	-	-	1	-	-	-	2
<u>L. camposi</u>	M -	-	-	-	-	-	-	1	-	-	-	1
	F -	-	-	-	-	1	-	1	-	-	-	2
<u>L. trapidoi</u> ^c	M -	-	-	-	-	-	-	1	-	-	-	1
	F -	-	-	-	-	-	-	-	-	-	-	1

^a A dash indicates that no specimens were encountered.

^b The females of these two species were not distinguished.

^c Single specimens of the following species were also taken: L. caprina, L. hartmanni, L. saulensis, L. verrucarum group, L. panamensis, L. serrana, L. nordestina, and L. gomezi.

ably larger number of specimens of L. trinidadensis, L. bifoliata, L. abonnenci (Floch and Chassignet), and L. shannoni (Dyar) were taken at tree 6 than at any of the other trees. However, in general the number of specimens of L. trinidadensis taken at each of the trees was rather similar; whereas L. bifoliata was quite localized with a majority of its specimens being taken from just one tree.

PHLEBOTOMINAE

DISCUSSION

Definition of Terms

For clarity, the following terms are defined according to the sense in which they are used in this paper. Assemblage is defined as a group of taxonomically similar populations living within a delimited and relatively uniform geographic area. Hence, the phlebotomine sandfly assemblage includes all of the species of phlebotomine sandflies which occur in the Providencia study area. Community is considered to be more encompassing, i.e., all of the plant and animal assemblages of a given area functioning "as a unit through coupled metabolic transformations" (Odum 1971). The term component is used to identify one or more populations that have a unique trait such as a behavioral characteristic. Thus, the anthropophilic species of the phlebotomine sandfly assemblage are commonly referred to as the anthropophilic component. The adjective anthropophilic is used in its literal sense, i.e., attracted to man, and thus does not imply that man is the preferred host. Species composition refers to the proportional representation of the species for a given catch or group of catches.

Comparison of Faunas

The phlebotomine sandfly assemblage of the Providencia study area is closely related to the Panamanian fauna. Thirty-one of the 35 identified species from the Providencia study area occur in Panamá (Christensen, 1972).¹ Interestingly, the four Providencia species, L. bifoliata, L. cirrita, L. orsonoi, and L. yuilli, which have not been found in Panamá are all known to bite man. Relatively few light trap collections were studied; therefore, the actual number of species occurring in the Providencia study area is probably larger than that given in Appendix C.

Since the same collecting methods, i.e., light traps, aspiration from tree trunks, and man-biting catches, were used at a site in Panamá (Chaniotis et al. 1971a and b), at a site in the Department of Chocó, Colombia (Young 1971), and at the Providencia study area, a comparison of species compositions seems valid. The Panamá and Chocó sites will be described in succeeding paragraphs. Thirty-seven species were identified at the Panamá location; 33, at the Curiche, Chocó site; and 35, in the Providencia area. Of the 35 species found in the Providencia area, 21 (60%) occurred in the Panamanian study area and 23 (66%) were found at the

¹This includes L. nocticola Young which is a recent addition to the Panamanian fauna (D. G. Young, personal communication).

Chocó site. The Chocó site had 22 (67%) of its species in common with the Panamanian site. In addition, 16 of the 19 species listed in the Río Raposo study (Department of Valle, Colombia) (Barreto 1969) occurred in the Providencia study area. The Río Raposo study had 15 species in common with both the Chocó and Panamanian sites.

In spite of the rather high degree of similarity in species composition between the Providencia, Chocó, and Panamanian sites, the anthropophilic components were rather distinct, especially with regard to the predominant species. In the forest series of catches at the Providencia study area, the predominant man-biting species and the percent of the catch attributed to each were L. hartmanni, 56%; L. trapidoi, 22%; and L. yuilli, 13%. Species taken less frequently included L. panamensis, 3%; L. tintinnabula, 1%; L. bifoliata, 1%, L. gomezi, 1%; and W. rotundipennis, 1%. The only other quantitative data on the man-biting activity of Phlebotominae in Colombia are those of Young (1971) who made a series of human biting collections at four sites in the Department of Chocó between March and December of 1967. These catches are not strictly comparable with mine since they were made primarily at ground level and only between 1830 and 2100 hours. However, these catches do indicate that the anthropophilic component in northwestern Chocó was considerably different from that of the Providencia study area in east central

Antioquia. The most extensive series of catches (3,763 specimens) was made in a "mixed evergreen forest" about 0.5 km from the Pacific coast and at an elevation of between 1 and 12 m. The predominant species and the percentage of the total catch attributed to each were L. panamensis, 47%; L. hartmanni, 19%; L. sanguinaria (Fairchild and Hertig), 11%; and L. recurva Young (reported as sp. "A"), 10%. Species taken less frequently included L. pessoana (Barretto), 4%; L. tintinnabula (reported as L. ayrozai) [Barretto and Countinho], 4%; L. geniculata (Mangabeira), 3%; and L. trapidoi, 1%. A small series of catches, made at a site about 3.5 km farther inland and at an elevation of 302 m, gave rather similar results although L. trapidoi accounted for 7% of the catch and L. recurva, only 3%. Another small series of catches was made in a "semi-cleared primary forest" which periodically became flooded. This forest was about 52 km from the Pacific coast and was at an elevation of 35 m. L. panamensis accounted for 87% of the 588 specimens taken at this site; L. pessoana accounted for 7% and L. hartmanni, 2%.

The most comprehensive study of the man-biting activity of Phlebotominae in Panama is that of Chaniotis et al. (1971b). Their study was made in a mature forest characterized as transitional between tropical moist forest and tropical dry forest. The elevation varied from about 50 to 180 m. The mean annual rainfall of this area is 204 cm and

there is a distinct dry season. Their catches were made both on the ground and in the canopy. The predominant species and the percent of the total catch attributed to each were L. pessoana, 40%; L. traidoi, 38%; and L. panamensis, 12%. Species encountered less frequently included L. sanguinaria, 6%; L. gomezi, 2%; L. olmeca (Vargas and Diaz Najera), 1%; and L. ylephiletor, 1%.

The anthropophilic component at the Providencia study area was very distinct from those of more distant regions where studies have been made. With the exception of L. panamensis and L. shannoni, the man-biting species encountered in Belize by Williams (1966 and 1970a) were different from those of the Providencia area. Although L. shannoni was commonly found resting on tree trunks at the Providencia study area, it was rarely taken in the biting catches. L. olmeca, a species which feeds primarily on small terrestrial mammals (Williams 1965, Disney 1968, and Lewis 1975a), was occasionally taken in the man-biting catches in Belize and rarely in the Providencia area. Studies in the Serra dos Carajás, Pará State, Brazil by Ward et al. (1973) also revealed a very different anthropophilic component. L. gomezi and L. shannoni were the only man-biting species that the Brazilian and Providencia areas had in common. All of the species taken in ground level man-biting catches in Surinam by Wijers and Linger (1966) were different from those occurring at the Providencia

study area.

Man-biting Activity in the Forest:
Vertical Stratification and
Between-site Differences

The vertical stratification of each species' biting activity tended to be quite variable between the three forest sites and thus a discussion of vertical stratification necessarily includes between-site differences. Differences in biting activity by individual species between the forest sites may be due either to simply a greater amount of biting activity at one site relative to another or to distinct variations in vertical stratification. To varying degrees these differences usually occur together as in the case of the biting activity of L. hartmanni at the Tiroteos site relative to the other forest sites. The modified geometric mean catches of L. hartmanni at the Buenos Aires and Providencia sites were over twice as large as that at the Tiroteos site (Table II-19). In addition, the biting activity of this species at the Tiroteos site was detected to be significantly greater in the understory than in the canopy (Table II-8) while at the other sites it was significantly greater in the canopy relative to the understory.

The detection of a significantly greater amount of biting activity in the canopy relative to each of the other levels for all species and sites combined (Table II-27) can

be attributed to the distinct preference exhibited by nearly all species for the canopy at the Providencia site (Table II-30). The biting activity of each of the four most abundant forest species, L. hartmanni, L. trapidoi, L. yuilli, and L. panamensis, was declared to be significantly greater in the canopy than at ground level (Table II-27), and with the exception of L. trapidoi, this was largely a result of their marked preference for the canopy at the Providencia site (Table II-33). The vertical stratification and between-site variability of biting activity by individual species will be elaborated upon in the discussion of each species.

Other studies of vertical stratification using humans as bait have shown the biting activity of all species combined to be either rather similar between levels (Johnson et al. 1963, Williams 1970a, and Chaniotis et al. 1971b) or distinctly greater at ground level (Ward et al. 1973). The pattern of vertical stratification obtained by Williams (1970a) in an area of "medium bush" in Belize was ground, 29%; understory, 36%; and canopy, 35%. L. panamensis was the only one of the common species in his catches that showed a preference for the forest floor. In Panama, Chaniotis et al. (1971b) found the magnitude of biting activity at the ground and canopy levels to be quite similar (ground, 51%; canopy, 49%) for all species combined. Two of the three most abundant species in their study

showed a strong preference for the forest floor. Ward et al. (1973) have described a 4-hour catch they made in Pará State, Brazil in which biting activity was distinctly concentrated at ground level. The vertical stratification of phlebotomine sandfly biting activity has also been studied by using animal-baited traps (Thatcher 1968, Disney 1968, Williams 1970a, and Shaw et al. 1972).

Buenos Aires 1 forest site. At the Buenos Aires site, man-biting activity was dominated by the three predominant forest species, i.e., L. hartmanni, L. trapidoi, and L. yuilli. In addition to these three species, the canopy catches frequently contained L. panamensis. The species composition of the understory catches at this site was quite similar to that of the canopy, although the magnitude of biting activity of each species was substantially reduced (Tables II-8 and II-9). However, at ground level the species composition tended to be somewhat different from that of the canopy and understory. This variation can be primarily attributed to the substantially lower percentage of L. trapidoi relative to L. hartmanni and the frequent presence of L. tintinnabula.

The terrain of the Buenos Aires forest was steeply sloped in the vicinity of the platform sites, and as a consequence the canopy was uneven and rather broken. Since the canopy did not provide a continuous closed layer, the microclimatic differences between the canopy and the lower

levels were somewhat reduced. There were scattered areas where fairly intense light penetrated to the forest floor as was evidenced by the presence of a few herbaceous plants including species of the Araceae and Marantaceae in the undergrowth. In this type of an environment the acceptable microclimate of an arboreal species is likely to be vertically broadened. This would appear to account at least in part for the relatively high amount of biting activity that occurred at ground level, especially by L. hartmanni. However, one might also expect that the amount of biting activity in the understory by arboreal species such as L. trapidoi would be somewhat higher than that for the forest floor (Table II-9).

Tiroteos forest site. With regard to species composition, the canopy and understory catches at the Tiroteos site were quite similar to the Buenos Aires canopy catches. The most noticeable differences were that at the Tiroteos site the ratio of L. trapidoi to L. hartmanni approached unity and there was a somewhat greater abundance of L. bifoliata. The ground level Tiroteos catches were quite similar in species composition to those of the Buenos Aires site. The most apparent difference was the greater abundance of L. tintinnabula in the Buenos Aires catches. The magnitudes of biting activity of L. hartmanni, L. trapidoi, and L. yuilli at the canopy and ground levels at the Tiroteos site were considerably lower than those at the Buenos

Aires site (Tables II-9 and II-18).

Previous disturbance by man was most noticeable in the Tiroteos forest. Some selective cutting in the past, not apparent in the immediate environs of the platform, has resulted in a reduced density of large trees and an incomplete upper canopy in portions of the forest. In addition, the site is located near the top of a south-facing slope. This somewhat drier environment may be less suitable for larval development and adult survival (Johnson and Hertig 1961 and Chaniotis 1975).

With an incomplete upper canopy, environmental differences between the canopy and the understory are likely to be reduced, and as a result differences in both the species composition and magnitude of biting activity between these two levels would also tend to be diminished. This is apparently what has happened at the Tiroteos site (Tables II-8 and II-9). Haddow (1961a) has observed a similar pattern of vertical distribution by the diurnal, arboreal Aedes longipalpis (Grünb.) in an African rain forest with a relatively open canopy. For a number of diurnal arboreal mosquitoes in Panama, Trapido and Galindo (1957) have found that the percentage of biting activity occurring in the canopy is greater in rain forest than in tropical deciduous forest. They have also observed that arboreal mosquitoes may be found near the forest floor where the canopy has been broken by a small clearing which need be no larger

than that resulting from the removal of a single large tree. Although some environmental parameters such as relative humidity and light may be the same throughout much of the night at all levels within a rain forest, most individuals are apparently able to orient to a preferred vertical level. Thus, when environmental differences between the canopy and understory are reduced by an open canopy, nocturnal, arboreal species also tend to have a broader vertical range of biting activity.

Providencia forest site. At the Providencia site, differences in both the magnitudes of biting activity and species composition of the catches were most pronounced between the canopy and the other two levels. As previously noted, the biting activity of L. hartmanni, L. trapidoi, and L. yuilli was markedly concentrated in the canopy at the Providencia site. In addition to these three species, L. gomezi, L. panamensis, L. bifoliata, and W. rotundipennis were present in nearly all of the canopy catches. The presence of L. gomezi and W. rotundipennis is thought to reflect this site's proximity to a clearing. The ground and understory catches at the Providencia site appeared to be quite similar, both in species composition and abundance. The biting activity of L. trapidoi, L. yuilli, L. bifoliata, and L. gomezi at these two levels was greatly reduced from that occurring in the canopy. L. panamensis was also taken with considerably less frequency at

the understory and ground levels. In fact, W. rotundipennis was the second most numerous species on the forest floor. The frequent occurrence of W. rotundipennis and the sporadic presence of L. yuilli and L. tintinnabula distinguished the ground level catches of the Providencia site from those of the other two sites.

Although the Providencia site was located on a steep hillside, the slope in the vicinity of the platforms was gentle. The upper canopy was quite dense, and thus even though this site was situated only about 50 m from a large clearing, the lower levels were well shaded. Since change in a vertical microclimatic gradient is likely to be more abrupt immediately beneath a closed upper canopy than beneath a relatively open one, the environmentally preferred range of a canopy species would tend to be more sharply delimited and vertically compressed in a forest with a dense upper canopy. Thus, an arboreal species would be expected to have a very high percentage of its biting activity in the canopy of such a forest. However, this appears to only partially account for the patterns of vertical stratification at the Providencia site, and other ecological factors related to the site's proximity to a clearing are suspected of also exerting considerable influence.

Summary of forest man-biting activity. The species composition of the forest catches was most dissimilar

between the ground and canopy microenvironments. The degree to which the understory catches resembled those for the ground and canopy levels appeared to be at least partially dependent upon forest structure. Thus, when the forest canopy was relatively open (Tiroteos site) the understory catches tended to more closely resemble the canopy catches, but when the canopy was unbroken and dense (Providencia site) the understory catches were more similar to those on the forest floor. The canopy catches at all three sites were composed primarily of L. hartmanni, L. trapidoi, and L. yuilli. Biting activity on the ground and in the understory was dominated by L. hartmanni. The only anthropophilic species distinctive to the forest floor was L. tintinnabula; however, this species was taken in relatively low numbers and was seldom encountered at the Providencia site.

For most species, variations in the magnitude of their man-biting activity from one site to another were greatest at the canopy and ground levels. Biting activity in the canopy by the three predominant forest species was of a greater magnitude at the Buenos Aires and Providencia sites than at the Tiroteos site, while on the forest floor the biting activity of these species was greater at the Buenos Aires site than at either of the other two locations. Most of these differences were detected to be statistically significant (Table II-18). In the understory,

between-site variations in the magnitude of the biting activity of L. hartmanni and L. trapidoi were slight.

Man-biting Activity in the Clearing

Very little attention has been given to the biting activity of Phlebotominae in clearings adjacent to forest. Chaniotis and Correa (1974) found man-biting activity within the center of a small clearing (25 x 30 m) to be only one-fifteenth of that at a site 50 m away in the forest. Phlebotomine sandfly biting activity was also reduced within the clearing habitat studied by us, but the reduction tended to be less than that described by the above authors. The clearing catches were made at six different microenvironments within a rather large clearing (approx. 17.5 hectares) adjacent to the Providencia forest. The catch sites have already been described in some detail, but it is worth emphasizing that the vegetation within the clearing was diverse and included pasture, cultivation, pioneer, and early secondary forest. In general the magnitude of biting activity varied considerably between the sites and the pattern of variation was not the same for all of the species. Figs. II-8 and II-9 suggest that there is a more or less continuous, albeit interrelated, variation in species composition between the clearing sites in approximately the following order: D, E, F, C, and B. The biting activity at site A was strongly dominated by L.

hartmanni, and the irregular and meager occurrence of other species has resulted in a rather widespread distribution of the catches for this site over the left half of Fig.

II-8.

Total biting activity at the two edge sites, D and E, was greater than that at the sites within the clearing and the difference was declared to be highly significant (Table II-23). Site D was located just within the pasture at the margin of mature forest and was only about 40 m away from the Providencia platform site. Site E was situated just within the pasture at the margin of a 10 to 15 m tall early secondary forest which merged about 100 m away with mature forest. The significantly greater magnitude of biting activity at the two margin sites can be primarily attributed to L. hartmanni which exhibited a preference for the margin sites even though it was the most numerous species at all of the clearing sites. The biting activities of L. trapidoi, L. yuilli, and L. panamensis were also concentrated at the two margin sites but these species were much less abundant at these sites than L. hartmanni. The biting activity of each of the three prominent forest species, i.e., L. hartmanni, L. trapidoi, and L. yuilli, was somewhat greater at site E than at site D. These differences can be primarily attributed to a single large catch of all three species at site E in March. The biting activity of L. gomezi was also greater at site E than at site D

but the difference was declared to be highly significant (Table II-23). This disparity is thought to be a reflection of the relatively sheltered nature of site D. Thus, the environment of this site appeared to be rather similar to that of the forest floor, a location where L. gomezi was seldom encountered. W. rotundipennis, which did not exhibit a distinct vertical preference at the Providencia site, and L. panamensis were taken in larger numbers at site D than at site E.

At clearing site F the modified geometric mean catches of L. hartmanni, L. trapidoi, and L. yuilli were of intermediate magnitude, i.e., they were less than those at the two edge sites but greater than those at sites C, B, and A where their biting activity tended to be sharply reduced. An exception was the biting activity of L. hartmanni at site B which was similar in magnitude to that at site F. L. gomezi and W. rotundipennis were, respectively, the second and third most abundant species at site F, and each had comparatively high magnitudes of biting activity at this site. Clearing site F was situated just within the pasture adjacent to a strip of pioneer vegetation that extended from the mature forest about 130 m away.

Total biting activity at clearing site C was considerably reduced and was detected to be significantly less than at site E, 40 m away (Table II-23). Clearing site C was located centrally within the pasture between sites E

and F and 30 to 40 m away from other vegetative formations. Most of the biting activity at site C was by L. hartmanni and L. gomezi. However, on a comparative basis the biting activity of L. hartmanni at this site was detected to be significantly less than that at sites E and D (Table II-23), and the modified geometric mean catch was only about half as large as that for sites F and B (Table II-22). There thus appears to be a genuine reluctance on the part of L. hartmanni to enter cleared areas, although it may be quite common in early successional stages adjoining mature forest. L. gomezi had a relatively high magnitude of biting activity at site C and almost exceeded L. hartmanni in terms of actual numbers taken. W. rotundipennis accounted for most of the remaining biting activity at this site (Table II-22). The greater biting activity of L. hartmanni, L. trapidoi, and L. yuilli at site F compared with site C suggests that these forest species extended well into the clearing along a narrow strip of pioneer vegetation extending from the forest, albeit at relatively low magnitudes, but were very reluctant to enter the pasture.

Total biting activity at clearing site B was slightly greater than at site C but was strongly dominated by L. hartmanni. This site was situated within a small grove of fruit trees in an area of diverse cultivation and was approximately 240 m away from mature forest. The modified geometric mean catch of L. hartmanni was about twice as

large for this site as it was for site C (Table II-22). The catches for site B form a rather distinctive cluster in Fig. II-8 indicating they have a rather unique species composition. This can be attributed to the strong dominance of L. hartmanni, relatively little biting activity by L. gomezi and W. rotundipennis, and a virtual absence of L. trapidoi, L. yuilli, and L. panamensis.

Man-biting activity by phlebotomine sandflies at clearing site A was considerably lower than that at any of the other clearing sites (Table II-21) and was strongly dominated by L. hartmanni. This site was located at the edge of an early secondary woods and was adjacent to the Río Anorí. Site A was approximately 360 m from the mature forest adjacent to site D and was about 280 m from mature forest to the southwest. The Scheffé pairwise comparisons for all species combined detected statistically significant differences between the magnitude of biting activity occurring at site A and that at sites D, E, and F (Table II-23). Although L. hartmanni accounted for 77% of the specimens taken at site A, the modified geometric mean catch of this species was quite small, being comparable only to that for site C. As mentioned earlier, the biting activities of all other species at this site were very low.

Following the clearing of a small portion of forest as for subsistence farming, Phlebotominae biting activity within the clearing appears to be dependent upon the

subsequent use of the land and whether there is additional clearing of the adjacent forest. Clearing site C can be considered representative of a cleared area that is not allowed to proceed to a secondary successional stage and thus can also be considered as a recent clearing. At this site there was a pronounced reduction in biting activity by the predominant forest species. The failure of L. hartmanni to dominate the biting activity at this site coupled with substantial biting activity by L. gomezi and W. rotundipennis resulted in this site having a comparatively high species evenness. If a portion of the clearing is neglected and pioneer vegetation becomes established, the anthropophilic component may become similar to that observed for site F. Although total man-biting activity was somewhat reduced compared with that at the forest edge, diversity of biting activity was greatest at this site. The estimate of the evenness of biting activity was also relatively large for this site. This was the result of a relatively moderate magnitude of biting activity by the forest species and comparatively high magnitudes of biting activity by the clearing species, i.e., L. gomezi and W. rotundipennis. The somewhat reduced diversity at site D at the edge of the mature forest is at least partially due to the dominance of L. hartmanni.

There is some indication from our studies that those forest species which show a strong vertical microhabitat

preference with regard to biting activity, e.g., L. trapi-
doi and L. tintinnabula, are less tolerant of any of the
clearing microenvironments than those species with somewhat
weaker preferences, such as L. hartmanni. The low values
for diversity and evenness at sites A and B are a result of
the strong dominance of L. hartmanni at these sites which
in turn can be at least partially attributed to reductions
in biting activity by the other species, especially at site
A. This is thought to be more a reflection of the distance
of these sites from mature forest than of the particular
type of vegetation surrounding the sites.

Variations in the Species Composition
of the Anthropophilic Component
between Different Microenvironments

Statistical comparisons were not made between the for-
est and clearing catches because of insufficient uniform-
ity between these two series of catches. However, the
polar ordination and informal comparisons, such as of the
modified geometric mean catches, reveal a number of inter-
esting differences. The comparisons between the forest and
clearing catches should generally be considered with some
reservation, especially since the clearing catches were
made only over a 6-month period and only at one level. The
6-month interval over which the clearing catches were made
extended from March to August and thus included one month

of the indistinct dry season.

A total of nine microenvironments were sampled in the night series of forest catches, i.e., the ground, understory, and canopy levels at each of three sites, and six additional ground level microenvironments were sampled in the clearing series of catches. The polar ordination compared and ordinated individual catches made in the above 15 microenvironments on the basis of the occurrence and relative abundances of the eight most frequently encountered species. Variations in species composition between the microenvironments were then expressed graphically. The resulting patterns in Figs. II-8 and II-9, derived from the first three ordination axes, suggest certain relationships between species composition and microenvironment which may be related to specific types of vegetation. Figs. II-8 and II-9 are somewhat skewed in favor of species presence rather than abundance since a square root transformation was applied to all of the values. This, of course, has tended to minimize the difference between catches with large and small values for the same species and was done to reduce the dominating influence of L. hartmanni on the analysis.

Fig. II-8 of the first two ordination axes shows the catches for the forest and clearing sites to be quite distinctly separated from each other. This indicates, on the basis of species composition, that the microenvironments

sampled at all three forest sites tended to exhibit a greater degree of similarity to each other than to the clearing microenvironments, and conversely the clearing microenvironments tended to be more closely related to each other than to the forest microenvironments.

The largest intercatch distances in Fig. II-8 appear to be between the canopy and understory catches at the Buenos Aires and Tiroteos sites on the one hand and clearing site C, the most exposed site, on the other. The catches at these forest microenvironments were quite similar, being composed primarily of L. hartmanni, L. trapidoi, and L. yuilli. The biting activity at clearing site C was dominated by L. hartmanni and L. gomezi and to a lesser degree by W. rotundipennis. The first axis of the ordination has essentially separated the forest catches from those of the clearing on the basis of the combined biting activities of L. trapidoi and L. yuilli relative to L. hartmanni. This has had the effect of placing most of the catches for the two edge sites, D and E, near the center of the first axis with many of the ground level forest catches which tend to have reduced amounts of L. trapidoi and L. yuilli. Thus, in Fig. II-8 the catches for clearing site D tend to be situated between those for the Providencia and Tiroteos ground level and the Providencia understory microenvironments and those for clearing sites E and F. Many of the clearing site catches have been separated from

the ground level forest catches by the second axis which reflects a general reduction in the dominance of L. hartmanni in the biting catches from the forest floor to clearing sites C, F, and E.

The species composition of the canopy catches tended to be quite dissimilar from that of either the ground level or clearing catches. An important difference was in the ratio of L. hartmanni to L. trapidoi and L. yuilli combined. This ratio was closer to unity for the canopy catches than for those of the forest floor and clearing sites where the ratios tended to be decidedly in favor of L. hartmanni. The biting activity of L. trapidoi was primarily restricted to the forest canopy. This species was very reluctant to enter the clearing. In the clearing catches L. trapidoi was taken most often at the two edge sites, and the modified geometric mean catches of L. trapidoi for these sites were comparable only to that of the very reduced ground level mean catch for the nearby Providencia forest site. The biting activity of L. yuilli also tended to be concentrated in the canopy. However, this species was frequently taken at ground level in the relatively open Tiroteos forest and at the edge of the early secondary forest, but like L. trapidoi, it was seldom taken at the sites within the clearing.

L. gomezi and W. rotundipennis were distinctive to the clearing habitat and the nearby Providencia forest site. Within this forest the biting activity of L. gomezi

was concentrated in the canopy. This species was taken infrequently in the understory and on the forest floor and also occurred in relatively low numbers at the margin of the forest 40 m away (site D). The variation in biting activity across the clearing sites indicates that L. gomezi favored the early secondary forest but also readily entered the pasture. The relatively low magnitudes of biting activity of L. gomezi, and for most of the other species at clearing sites A and B which were over 200 m from mature forest, suggest that these species may be dependent upon forest to provide a suitable microclimate for the development of the immature stages. The patterns of man-biting activity exhibited by L. gomezi, including its distinctly crepuscular diel pattern, suggest that this species may be more likely to come in contact with man than any of the other species and should be considered as a potential vector of human disease, at least at the Providencia study area. Although not as abundant as L. gomezi, W. rotundipennis was quite common in the clearing catches and appeared to be rather uniformly distributed over much of the clearing. This species was also frequently taken at the Providencia forest site where it maintained a rather uniform intensity of biting activity over all three vertical levels but was rarely encountered at the other two forest sites. The modified geometric mean catch of W. rotundipennis for each of the clearing sites, except for A, exceeded that for each

of the three vertical levels of the Providencia platform site by as much as 2.5 times.

A comparison of the modified geometric mean catches of L. panamensis for the clearing and forest sites (Tables II-19 and II-22) indicates that this species had relatively uniform magnitudes of biting activity in both habitats but was most numerous at the ecotonal microenvironments. In Venezuela, Pifano et al. (1960) have observed L. panamensis to be abundant at the forest perimeter, especially in areas where trees are being cut.

While making comparisons of biting activity between various forest and clearing sites, we have assumed that the catches obtained at these locations were typical of the microenvironment in which they were made. However, this may not always have been the case as we did not have sufficient resources to implement the night catches at more than one location in the three forests and in the six clearing microenvironments sampled. Highly localized variations in population density and biting activity have been observed for phlebotomine sandflies (Chaniotis et al. 1971a, Lewis 1971, and Shaw and Lainson 1968) and similar variations have also been noted for mosquitoes by Galindo et al. (1950).

Selection of Microenvironment

The vegetation of rain forest and its secondary successional communities create a number of microenvironments with their own microclimates. Temperature and humidity measurements made by us were not of sufficient frequency and precision to relate to biting activity. Within rain forest the microclimates near the ground and in the canopy are quite dissimilar during the day (Allee 1926, Haddow et al. 1947, Haddow and Corbet 1961, Richards 1952, and Allen et al. 1972). Microclimatic differences at the various strata beneath the upper canopy are dependent upon forest structure, and the climatic gradient from the canopy to the forest floor may be either continuous or discontinuous (Richards 1952). At night, temperature, saturation deficit, and light become quite similar at all levels within the forest (Haddow et al. 1947, Haddow and Corbet 1961, and Richards 1952). Just above the canopy and in adjacent clearings, these climatic factors may also be quite similar at night to those within the forest (Haddow and Corbet 1961, Haddow 1945). Many nocturnal Phlebotominae and Culicidae of the humid tropics have distinct microenvironmental preferences with regard to their biting activity and are able to orient to a preferred microenvironment in spite of similar temperature, humidity, and light regimens. Selection mechanisms for particular microenvironments with regard

to nocturnal biting activity are poorly understood. A species' distribution could be related to host preference with microenvironmental selection enhanced by the ability to distinguish slight microclimatic variations. However, Tesh et al. (1972) have shown that host selection by at least some rain forest Phlebotominae is strongly influenced by host availability. Variations in the patterns of vertical distribution exhibited between the three forest sites used in our study suggest that the species may have been responding to differences in forest structure which may have been manifested in microclimatic variation. A number of other factors may also influence the microenvironmental preferences for biting activity exhibited by a given species and include diurnal resting sites, proximity of carbohydrate source, flight range, physiological state, and heredity. Local variations in the abundance of phlebotomine sandfly populations have been related to edaphic conditions by Chaniotis et al. (1971a).

Diel Periodicity of Man-biting Activity

The diel periodicity of biting activity of the Neotropical species has been investigated to varying degrees by the following authors: Thatcher and Hertig (1966), Wigers and Linger (1966), Williams (1966 and 1970b), Shaw and Lainson (1968), Sherlock and Guitton (1969), and Chaniotis et al. (1971b). Extended catches, i.e., continuous

collecting over several hours, of phlebotomine sandflies in a forest environment have been made by Williams (1966 and 1970b). Williams used man as a bait and limited these catches to ground level. The most extensive study in Panamá of the diel periodicity of biting activity for anthropophilic species is that of Chaniotis et al. (1971b), although their collections were made at specific intervals rather than being continuous.

Diurnal biting activity. There was very little diurnal man-biting activity by the Phlebotominae in the Providencia study area. The biting activity of phlebotomine sandflies tends to be primarily crepuscular and nocturnal (Lewis 1971 and Chaniotis et al. 1971b), but diurnal biting activity near the forest floor has been reported from several regions (Williams 1966 and 1970b, Disney 1968, Chaniotis et al. 1971b, and Ward et al. 1973). In each of these instances, the daytime biting activity was dominated by a single species whose biting activity tended to be greater at night and occurred primarily at ground level. Thus, the absence of an avid man-biting species with a distinct preference for the forest floor appears to account for the paucity of diurnal Phlebotominae man-biting activity within the forests of the Providencia study area. L. tintinnabula was the only species taken in the man-biting catches that exhibited a distinct preference for the forest floor but it was encountered rather infrequently. Table II-14 indicates

that the meager diurnal biting activity in our study area occurred primarily at the ground and understory levels.

Reliability of summary temporal patterns in representing biting activity. A summarizing pattern of temporal biting activity such as Fig. II-12 for L. hartmanni represents the mean pattern of many catch nights and can be quite misleading. Haddow and Ssenkubuge (1973) have shown for the primarily nocturnal Anopheles gambiae Giles that its rather broad and ill-defined summary pattern of temporal biting activity obscured the fact that there was considerable night to night variation in the temporal pattern and concluded that "considerable caution must be used in this type of analysis, except in well synchronized biting patterns." A comparison of the nightly temporal patterns of biting activity for L. hartmanni, L. trapidoi, and L. yuilli revealed that each of these species also had a pronounced variation in its biting activity from one night to another. The summarizing patterns of these species are thus representative of biting activity only to the extent that they show the period of time in which biting activity is likely to be concentrated. However, biting cycles characterized by one or two consistent, narrow intervals of biting activity, such as occurs with crepuscular species, tend to be accurately represented by summary patterns. The biting activity of L. gomezi in the clearing (Fig. II-24) and of L. bifoliata in the forest (Fig. II-23) appears

to be of this type.

The nocturnal temporal patterns of biting activity.

Colless (1957) has related the rate at which Culex annulus arrived at a bait through the night to an equation for a constant rate of depletion. This was also expressed graphically as a depletion curve.² The equation presented by Colless, i.e., " $\log(K-C) = a + bt$ where K is the initial population, C the cumulative catch, t time, and a and b are constants" is thought to be limited to a rather unique situation in which a number of assumptions have been satisfied. Two assumptions were mentioned by Colless, i.e., random arrival at a host and a "'closed domain' . . . delimited by geographic features." The process of finding a host by a mosquito and presumably also by a phlebotomine sandfly is not likely to be an entirely random process. Gillies (1972) suggests there is an area of host-conditioned air, a host stream, that surrounds a host and tends to drift downwind from it. However, the encounter of a host stream may be a random process. In many instances, the vector popula-

²Colless (1957) and Kruijf (1972) use the term depletion curve to describe a component of the biting cycle. However, Gillies (1972) used depletion curve in a somewhat different sense to describe the familiar pattern in which there is an initial high rate of biting activity upon the introduction of a bait and then a rapid decline as the individuals in the proximity of the host stream become removed from the stimulated population. In this instance, depletion curve is used to describe the pattern of response to a sudden stimulus which is independent of the rhythmic biting cycle.

tion is likely to extend continuously for considerable distances around the host and a "closed domain" probably represents a rather specialized situation. Through local flight there would likely be considerable movement both into and out of the area surrounding the host, i.e., into the area where random encounter with the host stream could occur. The equation would also appear to be dependent upon the maintenance of a constant level of biting excitation by the population throughout the night which is unlikely to happen, e.g., consider the nocturnal biting activity of Anopheles gambiae as presented by Haddow and Ssenkubuge (1973) and that of L. hartmanni, L. trapidoi, and L. yuilli in this study. Relatively stable climatic conditions would seem to be another prerequisite.

Reduction in biting activity as a component of a biting cycle is likely to result from both the removal of individuals in the proximity of the host stream and a reduction in biting excitation. The frequent occurrence of sharp peaks in the temporal patterns of biting activity for individual nights coupled with the apparently limited flight range and localized distribution of phlebotomine sandflies (Chaniotis et al. 1974) suggest that the steep declines in biting activity which tended to follow these peaks were at least partially due to the depletion of individuals from the vicinity of the host stream. These sharp temporal peaks in biting activity also suggest that biting excitation

was frequently sudden, and comparisons of the nightly patterns (Figs. II-16, II-18, and II-19) indicate that they were variable with respect to time.

The large variability from one night to another in the temporal patterns of biting activity in the relatively stable nocturnal environment of a tropical wet forest is difficult to understand. Williams (1966) has suggested that the bimodal biting rhythms he detected for L. panamensis and L. shannoni may have been related to differences in the biting activity of nulliparous and parous individuals. Haddow and Ssenkubuge (1973) have discussed nocturnal biting cycles of mosquitoes, particularly in relation to the concept developed by Lumsden (1952) in which temporal variations in biting activity may be related to different age groups of the population. However, they noted that there was considerable evidence in the literature against this concept. Our superficial temperature measurements did not reveal any obvious relation between temperature and biting activity. Haddow and Ssenkubuge (1973) were unable to relate nightly variations in the biting cycle of the nocturnal Anopheles gambiae to relatively mild fluctuations in weather although the biting activity of this species was depressed by heavy rain and wind. The cues, environmental and/or physiological, that control the initiation and ascent components of a nocturnal biting cycle in the rain forest environment are largely unknown. Pifano et al. (1960) have

observed that phlebotomine sandflies disperse when the ambient temperature and humidity approach that of their diurnal resting sites. Scorza et al. (1968a) appear to hold a similar opinion. This dispersal may not be directly related to biting activity since there are several circadian activities dependent upon flight.

There was no indication of a consistent nightly vertical movement by either L. hartmanni, L. trapidoi, or L. yuilli. Neither the temporal patterns summarizing biting activity by vertical level (only the pattern for L. trapidoi is presented [Fig. II-20]) nor a night by night comparison of temporal patterns differentiated by level (Fig. II-17) gave an indication of such movement. Hadow (1961a, 1961b) has shown that the crepuscular mosquitoes Aedes ingrami Edwards and Mansonia fuscopennata (Theobald) make daily vertical migrations from the forest floor to the canopy. The diurnal resting sites of L. trapidoi have been investigated in Panama by Chaniotis et al. (1972). Their study indicates that the forest leaf-litter may be the preferred microhabitat for resting adults during the day; although a number of other microhabitats were also used including the lower part of tree trunks, a resting site apparently seldom used by this species in the Providencia area (Table II-36). Chaniotis et al. (1974) indicate that L. trapidoi moves upward at dusk into the canopy from these diurnal resting sites. This pattern of movement was not

apparent from our biting studies. On many nights the biting activity of L. traidoi was very low during the first few hours after sunset suggesting that this species may move into the canopy before reaching a high degree of biting excitation. One should also recall that the limited diurnal biting activity of this species was concentrated in the understory. This would suggest that L. traidoi may also rest in the understory and perhaps shaded areas near the canopy. An investigation of the diurnal resting sites of L. hartmanni and L. yuilli has not been made.

A comparison of the summary temporal patterns of biting activity for the forest and clearing catches indicated biting activity tended to occur earlier at the clearing sites than at the forest locations. This was true for L. hartmanni, L. traidoi, and L. yuilli although the forest and clearing patterns were quite similar for L. panamensis (Figs. II-12, II-13, II-14, and II-15). At the clearing sites variability in the temporal pattern of biting activity between individual nights appeared to be somewhat dependent upon the site as the temporal pattern of L. hartmanni at site E was considerably more variable than at site D, adjacent to the mature forest (Fig. II-18). The modified geometric mean catch of man-biting activity for all species combined during the first catch period after sunset was 1.5 times greater for the clearing sites than for the forest sites (Table II-26). However, there was considerable

variability in biting activity at this time between the individual clearing sites. The greater magnitude of biting activity in the clearing during the first hour after sunset can be largely attributed to the crepuscular L. gomezi. Within the forest only the relatively infrequent L. bifoliata exhibited a distinct crepuscular biting cycle. The tendency for biting activity to be concentrated earlier at the clearing sites than within the forest is difficult to rationalize, especially without precise climatic data. Furthermore, we do not know to what extent biting activity within the clearing is due to specimens that moved into the clearing on previous nights and found suitable diurnal resting sites and/or to what extent it is due to flight during the same night from the adjacent forest.

Seasonal Variations in Man-biting Activity

The seasonal patterns of man-biting activity presented in Table II-35 must be considered as rough approximations due to small sample size. In spite of sample size, seasonal fluctuations by the composite population were relatively mild, and in general the same was also true for L. hartmanni. L. panamensis exhibited the most pronounced seasonal fluctuation in man-biting activity, attaining a marked peak in June and July. Seasonal fluctuations in population density characterized by increases during the wet season and decreases in the dry season have been observed for many

species (Fairchild and Hertig 1951, Biagi and Biagi 1953, Johnson et al. 1963, Ortiz and Scorza 1963, Scorza et al. 1963, Disney 1968, Scorza et al. 1968b, Lewis 1971, Chaniotis et al. 1971a, and Christensen et al. 1972). A few species such as L. carpenteri (Fairchild and Hertig), L. cruciata (Coquillett), and L. permira (Fairchild and Hertig) appear to be more abundant during the dry season (Chaniotis et al. 1971a, Christensen et al. 1972, and Disney 1968).

The seasonal patterns are also perhaps somewhat atypical from the standpoint that there was an unusually large amount of rain during the 1971 dry season. Chaniotis et al. (1971a) have shown that total sandfly density in the dry season may be dependent upon the severity of this season. Thus, during an unusually mild dry season, they obtained considerably larger numbers of most species than they did during the previous dry season when the monthly totals of rainfall were substantially lower and resembled the 10-year mean. However, Chaniotis et al. (1971b) also found that the seasonal patterns of man-biting activity of the three predominant anthropophilic species in their study showed no clear relationship with estimates of population density obtained by other means in the same area over the same time. Accordingly, the seasonal patterns of man-biting activity in Table II-35 may not necessarily be accurate representations of population density.

Derivation of Interspecific
Differences in Biting Activity

The behavioral differences in biting activity observed between the various species in this study may have evolved more as a result of adaptive specialization than of competition. Downes (1971) considers the Phlebotominae to be one of the most archaic groups of modern Diptera. He suggests that forms similar to those currently in existence were present in the Triassic period, a time when reptiles were dominant and early mammals had not yet begun to develop. Phlebotominae-like species were thus in a position to evolve with the contemporary vertebrates and adapt to their habits. (Fossil evidence is inconclusive, however, with all authentic fossils of the Psychodidea apparently being from the Tertiary [Rohdendorf 1974].) This coevolution is apparent in our present species, some of which appear to be quite host specific and have morphological (Lewis 1975b) and behavioral adaptations which presumably enhance their success in obtaining a blood meal from a preferred host. The biting activity of others tends to be related to host availability, e.g., those utilizing a broad range of mammals (Tesh et al. 1972). However, even these species, e.g., L. trapidoi, may have distinct behavioral patterns related to biting activity. Differences between species which are related to biting activity are thus thought to have evolved primarily from sandfly-host interactions

rather than from interspecific competition between sandfly species.

The segment of the phlebotomine sandfly life cycle in which interspecific competition would most likely occur is not readily apparent. The larvae of many species develop on the forest floor, and at least some species have a preferred spatial niche such as the soil around certain trees (Rutledge and Ellenwood 1975a, c). While there would likely be an abundance of suitable spatial niches for larval development in a favorable environment, there may be few in a marginal one. Competition could therefore develop in marginal environments between two species utilizing rather similar spatial niches. The larvae of many forest species feed on mold and decomposing organic matter such as dead insects and leaf litter (Johnson and Hertig 1961). Competition for food among larvae is thus likely to be inconsequential. Very little information exists about the sugar feeding habits of adult sandflies in the Neotropical forest environment. Thus, the likelihood of competition for a carbohydrate source cannot be determined. Probable sources of sugar meals include nectar, honey dew, ripe fruit, and plant fluids which become accessible from damaged plant tissue. Competition for the blood of a vertebrate host utilized by two or more species would likely be minimal since the amount of blood taken, even by many individuals, would be insignificant compared to the total volume of blood present in a

host. Likewise, competition for space on most hosts would be minimal. Some partitioning of the host with respect to the location of biting activity may occur (Lewis 1971).

Species Using the Base of Trees
as a Diurnal Resting Site

The relatively high percentage of L. trinidadensis among the Phlebotominae aspirated from the tree bases was not surprising as this species has been found in a number of studies both in Panama and Colombia to be a dominant sandfly species of this microhabitat (Chaniotis et al. 1971, Young 1971, Chaniotis et al. 1972, and Christensen et al. 1972). These investigations also indicated that L. shannoni was a common constituent of the tree base sandfly component. In the Providencia study area L. shannoni and the closely related L. abonnenci appeared to utilize tree bases as diurnal resting sites to a similar degree. Although relatively common on tree bases sampled in the Providencia study area, L. bifoliata and L. spinosa (Floch and Abonnenc) were not encountered in the aforementioned studies. L. bifoliata was the only species taken with some degree of regularity in the man-biting catches that used the base of trees as a diurnal resting site in the study area. While L. trapidoi was found to frequently utilize tree bases as diurnal resting sites in Panama, albeit leaf-litter appeared to be the preferred resting site, by

Chaniotis et al. (1971a, 1972); it appeared to rarely use tree bases as a diurnal resting site in the Providencia study area. Collections from tree buttresses in the Department of Chocó, Colombia by Young (1971) revealed that L. trapidoi used this resting site rather infrequently, accounting for about 2% of the individuals encountered in this microhabitat.

The Common Man-biting Species of
the Providencia Study Area

L. bifoliata Osorno-Mesa, Morales-Alarcón,
de Osorno, and Muñoz de Hoyos, 1970

L. bifoliata is known only from Colombia and was described from a single male captured in the hollow of a tree at Puerto Boyacá, Department of Boyacá (Osorno-Mesa et al. 1970). The female has been illustrated by Young (1971) from specimens taken in the Providencia study area.

Although not abundant, L. bifoliata was taken primarily in the forest series of catches (Table II-5). It was encountered most frequently at the Providencia and Tiroteos sites (Table II-19). The biting activity of L. bifoliata occurred primarily in the canopy at the Providencia site, but its vertical stratification was less pronounced in the more open Tiroteos forest (Table II-12). The biting activity of L. bifoliata within the forest was primarily crepuscular; however, few individuals were encountered during the

period preceding sunrise. Although adults of L. bifoliata were present during every month of the year, the number of catches made was insufficient to reveal any distinct seasonal variations in its biting activity. L. bifoliata accounted for 22% of the phlebotomine sandflies collected from the base of trees and was the species encountered with the second greatest frequency in this microhabitat (Table II-36). However, its distribution appeared to be somewhat localized as a majority of the individuals of this species were taken at just one tree.

L. gomezi (Nitzulescu), 1931

L. gomezi has a widespread geographic distribution, occurring from El Salvador and Nicaragua to Brazil, Peru, and French Guiana (Fairchild and Hertig 1959, Young 1971, and Llanos 1973). This species appears to be quite widely distributed in Colombia and has been taken primarily at elevations below 800 m (Barreto 1969, Young 1971, and Osorno-Mesa et al. 1972a). Fairchild and Hertig (1948) indicated that in Panama this species bit man "both outdoors and in houses, even in quite urban areas . . . [and] it is probable that it is semidomestic."

A comparison of the modified geometric mean catches of L. gomezi for the forest and clearing habitats (Table II-5) shows that the biting activity of this species was concentrated in the clearing. Although comparisons between

the forest and clearing series of catches must be considered with some reservation, the difference appears to be of sufficient magnitude to indicate a definite preference by L. gomezi for the clearing habitat. In the forest catches, L. gomezi was taken almost exclusively at the Providencia site (Table II-20) which was located just 40 m away from clearing site D. Only one individual of this species was taken at the Tiroteos site which was almost one kilometer from the nearest clearing, and none were encountered at the Buenos Aires site, about 200 m from a clearing. In the clearing L. gomezi was taken in greatest numbers at site E which was at the edge of secondary forest and pasture. It was also quite common at sites F (edge of pioneer vegetation and pasture) and C (open pasture). Relatively small numbers of L. gomezi were encountered at site D which was at the edge of mature forest, and the difference in numbers taken between this site and site E was detected to be highly significant (Table II-23). Young (1971) has noted that over most of its range this species tends to occur in cultivated or semi-cleared areas. Johnson et al. (1963) and Thatcher and Hertig (1966) found L. gomezi to be quite common in an area that was rapidly being cleared. Johnson et al. (1963) also found it to be one of the two predominant species attracted to man and horse in an area of mainly secondary growth. However, L. gomezi was not taken by Chaniotis and Correa (1974) in a small series of man-biting

catches made in the center of a 27 x 33 m clearing.

At the Providencia platform site, L. gomezi was taken primarily in the canopy (Tables II-8 and II-11). Chaniotis et al. (1971b) obtained a similarly high percentage of man-biting activity by this species in the canopy relative to the forest floor. Johnson et al. (1963) also caught greater numbers of L. gomezi biting man at 11 m than at ground level. The limited study of the vertical distribution of phlebotomine sandflies by Ward et al. (1973) in the Serra dos Carajás, Pará State, Brazil, indicated that the biting activity of L. gomezi may also be primarily arboreal in that region. However, in an extensive series of light trap catches, Chaniotis et al. (1971a) obtained larger numbers of L. gomezi at ground level than in the canopy.

In the clearing habitat the man-biting activity of L. gomezi was primarily crepuscular (Fig. II-24). A distinct peak in biting activity tended to occur between 1800 and 2000 hours, and there was an indication of a smaller peak from 0500 to 0700 hours. The biting activity of L. gomezi at the Providencia forest site (Table II-32) was rather uniform throughout the night with only a slight indication of the distinctly crepuscular pattern observed in the clearing. The results presented by Chaniotis et al. (1971b) indicated that the man-biting activity of L. gomezi in the forest canopy was greatest at midnight and that there was very little biting at dusk.

There was an indication that the man-biting activity of L. gomezi was substantially reduced during the latter half of the rainy season, but due to the small sample size this could not be conclusively determined. In Panamá L. gomezi has been taken in greater numbers during the dry season than in the lengthier wet season by Johnson et al. (1963) from biting catches using man and horses, by Chaniotis et al. (1971a) from light trap collections, and by Chaniotis et al. (1972) from leaf litter, a diurnal resting site. For the same area and period of time in which the aforementioned light trap collections were made, Chaniotis et al. (1971b) also carried out a series of man-biting catches which gave quite different monthly estimates of the population density of L. gomezi. These catches showed the man-biting activity of L. gomezi to be greatest at the end of the rainy season and the beginning of the dry season. Rutledge et al. (1975) have noted that for certain localities in the Panamá Canal Zone the L. gomezi-L. panamensis association of sandflies occurred in the relatively wet part of the year.

L. gomezi has been shown to feed on a variety of mammals (Thatcher and Hertig 1966, Thatcher 1968, Tesh et al. 1971, and Tesh et al. 1972) and the domestic chicken (Thatcher and Hertig 1966). Johnson (1961) found that certain females of L. gomezi were autogenous and that reciprocal crosses with anautogenous individuals failed to produce

fertile eggs. In a study of diurnal resting sites, Chan-iotis et al. (1972) found adults of L. gomezi primarily on the leaf litter of the forest floor; however, it accounted for only about 12% of the specimens taken from that micro-habitat.

Johnson and Hertig (1961) have colonized L. gomezi and have determined the duration of the various developmental stages of the life cycle. These authors found that wild-caught females laid an average of 29 eggs and that the period of time from oviposition to adult emergence averaged about 34 days. Mirsa (1952) obtained rather similar estimates of the duration of the developmental stages of this species but found the average number of eggs per oviposition to be greater. Rutledge and Ellenwood (1975b, 1975c) observed that the sites of larval development for L. gomezi were more abundant in hilltop regions and tended to be associated with large Anacardium trees.

Schneider and Hertig (1966) have shown one of the leptomonad infections isolated from L. gomezi by Johnson et al. (1963) to be a strain of Leishmania braziliensis sensu lato.

L. hartmanni (Fairchild and Hertig), 1957

L. hartmanni appears to have a rather localized geographic distribution as it has only been found in Panamá and Colombia. This species has been taken at elevations varying from near sea level to at least 700 m. The known distribution of L. hartmanni indicates that it is primarily limited to forested areas in regions with high annual rainfall (Fairchild and Hertig 1957, Barreto 1969, and Young 1971). There is virtually no information in the literature about the man-biting activity of this species. L. hartmanni was encountered by Young (1971) in the series of man-biting catches which he made in the Department of Chocó, Colombia, and which have been described above. These catches were made primarily at ground level. At the Curiche forest site which was adjacent to the Pacific coast, L. hartmanni accounted for 19% of the individuals taken; but at a somewhat drier site in an area of "semi-cleared primary forest" about 52 km inland, this species accounted for only 2% of the total catch.

The large numbers of L. hartmanni taken at all of the forest and clearing sites reflect this species dominance of the man-biting activity in the Providencia area. Even though statistically significant differences were detected in the magnitudes of biting activity of L. hartmanni between the two edge sites and sites A and C within the clearing, it

was still the most numerous species at sites A and C. The ubiquity of this species in both the forest and clearing habitats is thought to result from it having a relatively broad microenvironmental tolerance which may have been further increased by a seemingly optimal environment. A species occurring in an area which is environmentally optimal is thought to have a wider microenvironmental tolerance than it would have in a less favorable area where it would tend to be limited to those microenvironments most closely approximating the optimum. Thus, in an optimal environment a species may have increased niche space.

When summarized over sites, the man-biting activity of L. hartmanni was detected to be significantly greater in the canopy than either in the understory or on the ground. However, the pattern of vertical stratification varied extensively between the three forest sites (Table II-8), and appeared to be influenced by forest structure. Biting activity in the canopy relative to ground level was not detected to be significantly different at the Buenos Aires and Tiroteos sites. However, it was declared to be significantly greater for the canopy level at the Providencia site where the biting activity of nearly all of the species was concentrated in the canopy. Comparisons of biting activity across the three forest sites (Table II-18) indicated that the magnitude of biting activity in the understory was similar at all three sites. However, a signifi-

AD-A049 853 WISCONSIN UNIV MADISON DEPT OF VETERINARY SCIENCE F/G 6/3
ECOLOGICAL AND AEROSPACE MEDICAL ASPECTS OF VIRUS DISEASES. PAR--ETC(U)
OCT 74 R P HANSON, T M YUILL AFOSR-72-2337
UNCLASSIFIED AFOSR-TR-75-1645-REV NL

WISCONSIN UNIV MADISON DEPT OF VETERINARY SCIENCE F/G 6/3
ECOLOGICAL AND AEROSPACE MEDICAL ASPECTS OF VIRUS DISEASES. PAR--ETC(U)
OCT 74 R P HANSON, T M YUILL AFOSR-72-2337

AFOSR-TR-75-1645-REV

NL

3 of 4

ADA049 853



cant difference was detected at ground level between the Buenos Aires site and the Providencia and Tiroteos sites and in the canopy between the Tiroteos site and the Buenos Aires and Providencia sites. When the temporal pattern of man-biting activity of this species was differentiated by level, no distinct patterns of vertical movement were found. However, there was a tendency for the biting activity to be concentrated at ground level between 1900 and 0100 hours and in the canopy between 2100 and 0300 hours.

The temporal pattern of the man-biting activity of L. hartmanni was quite variable between nights at both the forest and clearing sites. The individual night catches tended to have distinct but variable peaks in biting activity. When summarized over sites and levels, biting activity tended to be concentrated in the forest between 1900 and 0300 hours and in the clearing between 1900 and 2300 hours. The magnitudes of biting activity from sunset through 2100 hours were similar for both of the habitats but became substantially reduced in the clearing after that time. At the Buenos Aires site the biting activity of L. hartmanni tended to increase quite rapidly after sunset and to be concentrated between sunset and 0100 hours. At the other two forest sites, biting activity tended to increase at a more gradual rate after sunset and to be concentrated over a somewhat later period of time. In the clearing, between-night variation in the temporal pattern of biting

activity appeared to be somewhat dependent upon the site.

The monthly means presented in Table II-35 suggest that seasonal changes in the biting activity of L. hartmanni in the Providencia region may be mild. Biting activity during the dry season may have been higher than usual due to an abnormally large rainfall for that period.

L. panamensis (Shannon), 1926

L. panamensis appears to be indigenous to forested lowland areas, elevations ranging from near sea level to about 800 m, from southern Mexico and Belize to Colombia and Venezuela (Biagi and Biagi 1953, Fairchild and Hertig 1959, Williams 1965, and Osorno-Mesa et al. 1972). This species has also been reported from Brazil by Martins et al. 1963.

L. panamensis had rather similar magnitudes of biting activity both between and within the forest and clearing habitats. The modified geometric mean catches of this species for the forest and clearing habitats were almost the same (Table II-5). The greater number of specimens taken at the Providencia site compared with the other two forest sites (Table II-19) was due to a single large catch of 145 individuals on July 7, 1971. Significant differences in the magnitudes of biting activity were not detected between any of the clearing sites by the Scheffé pairwise contrasts (Table II-23). However, the number taken and the modified

geometric mean catch for each of the two edge sites were noticeably larger than those for sites A, B, C, and to a lesser degree, F (Table II-22).

Whether L. panamensis has a distinct preference for the forest-clearing ecotone is difficult to ascertain from the literature. In Venezuela Pifano et al. (1960) captured large numbers of L. panamensis at the forest perimeter, especially in areas where trees were being cut. Both Pifano et al. (1960) and Scorza et al. (1968a) indicate that this species flies from the forest periphery at dusk to human dwellings. My studies and those of Chaniotis and Correa (1974) show that L. panamensis is reluctant to enter clearings to bite man. However, as will become increasingly evident, the behavior of L. panamensis appears to be quite variable from one region to another.

L. panamensis is a common anthropophilic species in mature, disturbed, and secondary forest. In the Department of Chocó, Colombia, Young (1971) found that L. panamensis accounted for 44% of the evening (1830-2100 hours) ground level man-biting activity in a lowland "mixed evergreen forest" located less than a kilometer from the Pacific coast. This species accounted for 87% of the specimens taken in a similar series of catches made in a "semi-cleared primary forest" about 52 km inland and over approximately the same time period (April to December). However,

in terms of actual numbers taken per man hour, L. panamensis was only about one-third as abundant at the latter site. On the basis of light trap collections, Chaniotis et al. (1971a) found L. panamensis to be more abundant in a mature forest than in an adjacent secondary forest. Studies in a secondary forest by Johnson et al. (1963) revealed that L. panamensis was the predominant species attracted to man and horse during the rainy season. Ground level collections of phlebotomine sandflies using man as a bait were made at a number of forested areas in Belize by Williams (1965). In nearly all of the areas, L. panamensis was one of the dominant or subdominant species of the anthropophilic component. Disney (1968) indicates that the forests of Belize have been subjected to varying degrees of disturbance from both man and hurricanes.

The biting activity of L. panamensis for the three forest sites combined was declared to be significantly greater in the canopy than at either of the other two levels (Table II-7). This pattern of vertical stratification was most apparent at the Buenos Aires and Providencia sites, but at the Tiroteos site biting activity was rather similar in magnitude at all three levels (Table II-9). These patterns of vertical stratification differ markedly from those of previous studies where L. panamensis was found to bite primarily at ground level when either man (Fairchild and Hertig 1951; Johnson et al. 1963; Williams 1970a, 1970b; and

Chaniotis et al. 1971b) or animals (Disney 1968, and Thatcher 1968) were used as a bait. Williams (1970a, 1970b) and Christensen et al. (1972) have compared light trap collections made near ground level with those made near or within the canopy. They obtained much larger numbers of L. panamensis in the proximity of the canopy than they did near the forest floor. However, in the extensive series of light trap collections made by Chaniotis et al. (1971a), approximately three times as many individuals of this species were taken near the ground as in the canopy. Disney (1968) found L. panamensis to be one of the predominant species occurring under dead leaves on the forest floor. Williams (1970b), however, suggests these may have been recently emerged flies and believes his light trap results may indicate that older individuals of this species commonly rest on the foliage of trees. Chaniotis et al. (1972) sampled a number of diurnal resting sites of phlebotomine sandflies in a Panamanian forest and found that L. panamensis constituted about 10% of the individuals resting on the leaf litter of the forest floor and 1.5% of the individuals resting on green plants near the forest floor. Collections were also made from animal burrows and tree hollows and at varying heights on tree trunks, but few if any specimens of this species were obtained from these microhabitats.

The biting activity of L. panamensis within both the forest and clearing habitats (Fig. II-15) tended to be

concentrated in the interval from sunset to about 0200 hours. These patterns can be compared with those obtained by Williams (1966 and 1970b) for the ground level man-biting activity of this species in forested areas of Belize. In 1966, Williams reported on a short series of extended catches (each was 12-14 hours in duration) made at the end of a rainy season. The resulting temporal pattern showed a tendency for the man-biting activity of L. panamensis to be concentrated between 1800 and 2400 hours. Williams considered the pattern to be bimodal and speculated that such a pattern may be produced by variation in the time of biting activity of nulliparous and parous individuals. The results of a more extensive series of catches (Williams 1970b) indicated a distinctly bimodal pattern with a tendency for biting activity to be concentrated from 1700 to 0200 hours. The 1966 and 1970 temporal patterns were quite different from each other, suggesting that there may have been considerable between-night variation in the temporal pattern of biting activity. The temporal patterns presented by Williams (1966 and 1970b) also reveal that there was some diurnal biting activity, especially during the morning hours. L. panamensis was occasionally encountered in the diurnal series of forest catches at the Providencia study area (Table II-14). Chaniotis et al. (1971b) also detected a small amount of diurnal biting activity by this species at ground level.

Seasonal variation in the man-biting activity of L. panamensis was very pronounced. Although this species was taken in the biting catches every month, it attained a distinct peak in biting activity during the rainy season months of June and July (Table II-35). Fairchild and Hertig (1951) were perhaps the first to suggest that L. panamensis is primarily a rainy season species. Since then several studies have shown this to be true (Biagi and Biagi 1953, Johnson et al. 1963, Disney 1968, Chaniotis et al. 1971a, and Christensen et al. 1972). The studies of Disney (1968) and Chaniotis et al. (1971a) indicate that this species is most numerous during the first few months of the rainy season. The study by Chaniotis et al. (1971b) is an apparent exception as they found the man-biting activity of L. panamensis to be primarily concentrated in the dry season. Thus, the monthly estimates of the population density of L. panamensis derived from its man-biting activity (Chaniotis et al. 1971b) were quite dissimilar from those obtained for the same area by light traps (Chaniotis et al. 1971a).

L. panamensis appears to feed on a broad range of mammals (Thatcher 1968 and Tesh et al. 1972). Thatcher (1968) also found L. panamensis to be attracted to the domestic chicken.

Johnson and Hertig (1961) have determined for L. panamensis the length of time required to complete each of its

developmental stages and found that the period of time from oviposition to adult emergence averaged about 28 days. In Venezuela, Mirsa (1952) observed the emergence of adults 29 days after oviposition. Wild-caught females were found to lay an average of 28 eggs by Johnson and Hertig (1961) while Mirsa (1952) obtained an average oviposition of 58 eggs from five wild females.

Hanson (1961) and Johnson and Hertig (1961) indicate that decaying leaves and litter in well-shaded areas on the forest floor are the sites of larval development for L. panamensis. Rutledge and Ellenwood (1975b and 1975c) have shown that the forest litter and soil are modified by a variety of environmental factors which can influence the distribution of developing larvae. Thus "breeding populations" of L. panamensis were found to be greater in hill-top regions and to be associated with large Anacardium trees. Johnson and Hertig (1961) indicate that quiescence may occur in fourth-instar larvae of L. panamensis and is probably initiated by adverse conditions, especially a lack of moisture.

Christensen et al. (1969) isolated Leishmania brazil-iensis sensu lato from a wild-caught L. panamensis and confirmed its identity through infection of hamsters. Promastigote (leptomonad) flagellates have been found in this species by Pifano (1940), Pifano et al. (1960), Johnson et al. (1963) and Williams (1970b). Johnson et al. (1963)

found a comparatively low rate of leptomonad infection in wild-caught L. panamensis.

L. tintinnabula Christensen and Fairchild, 1971

L. tintinnabula has recently been described from a site in Panama situated less than 1.6 km from the Colombian border (Christensen and Fairchild 1971). The type specimens were collected in a "wet submontane forest" at an elevation of 600 m. Young (1971) has found this species in Colombia although at the time he considered it to be L. ayrozai. Most of his collections of this species were made in a "mixed evergreen forest" about 0.5 km from the Pacific coast in the Department of Chocó at an elevation of between 1 and 12 m. Barreto (1969) has reported the occurrence of L. ayrozai in the Department of Valle, Colombia, but this may also be L. tintinnabula.

The man-biting activity of L. tintinnabula occurred almost exclusively at the Buenos Aires and Tiroteos forest sites (Tables II-5 and II-19). Unlike the Providencia site which was only about 40 m within the forest, both of these locations were at least 200 m from the forest margin. Another distinctive characteristic of this species' biting activity was its marked preference for the forest floor (Table II-11). The biting activity of L. tintinnabula tended to be concentrated between 1900 hours and midnight (Fig. II-22). L. tintinnabula was one of the predominant

species in the light trap collections but was taken in relatively low numbers in the man-biting catches which suggests that it was reluctant to bite man. Although adults of L. tintinnabula were taken throughout the entire year, the number of catches made was insufficient to reveal any distinct seasonal variations in its biting activity. Young (1971) collected the majority of his individuals of this species in June, biting man.

L. trapedoi (Fairchild and Hertig), 1952

L. trapedoi has been found in Honduras, Costa Rica, Panamá, Ecuador (Fairchild and Hertig 1959), and Colombia (Barreto 1969). Its distribution resembles that of the Meso-American area of endemism of Martins and Morales-Farias (1972). This species has been recorded at elevations varying from near sea level to about 800 m (Fairchild and Hertig 1952, Barreto 1969, and Young 1971). Fairchild and Hertig (1952) indicated that in Panama L. trapedoi occurred primarily in forested areas with high annual rainfall.

A distinctive characteristic of the man-biting activity of L. trapedoi in the Providencia study area was its strong preference for the canopy. At all three forest sites, a highly significant difference was detected in its biting activity between the canopy and the ground (Table II-8). Highly significant differences were also detected

between the canopy and the understory for the Buenos Aires and Providencia sites. The distinct concentration of this species' biting activity in the forest canopy was first noted by Fairchild and Hertig (1952) and was demonstrated quantitatively by Thatcher (1968) and Chaniotis et al. (1971b). Johnson et al. (1963) also found that L. trapidoi bit man in greater numbers on tree platforms than at ground level.

Chaniotis et al. (1974) hypothesized that L. trapidoi moves into the canopy at dusk from diurnal resting sites on or near the forest floor. This vertical movement was not detected by our catches. The biting activity of this species for all sites combined was consistently greater in the canopy than at ground level. The infrequent diurnal biting activity of L. trapidoi occurred primarily in the understory.

The magnitudes of biting activity by L. trapidoi at the three forest sites were relatively similar, although the modified geometric mean catch at the Providencia site was almost twice as large as that at the Tiroteos site. When a comparison was made between the sites of the biting activity for the first seven night catch periods, no statistically significant differences were detected for all levels combined. Since a considerable proportion of the biting activity of L. trapidoi frequently occurred after the first seven catch periods (Fig. II-13), the pairwise

contrasts (Table II-18) should be considered with some caution. For individual levels, these contrasts did indicate that the biting activity of L. trapidoi in the canopy was significantly greater at the Providencia site than at the Tiroteos site. At ground level, biting activity was declared to be significantly greater at the Buenos Aires site than at either of the other two sites.

L. trapidoi bit man primarily in the forest canopy and was very reluctant to enter the clearing. The modified geometric mean catches for the two edge sites were, however, comparable with those for ground level at the Providencia and Tiroteos forest sites. L. trapidoi was rarely taken at sites A, B, and C within the clearing.

Within the forest the biting activity of L. trapidoi tended to be concentrated between 2300 and 0500 hours. However, there was considerable between-night variation in the temporal pattern, and on many nights there was a distinct peak in biting activity. The limited biting activity at the clearing sites occurred primarily before midnight.

The biting activity of L. trapidoi tended to be quite variable from one month to the next, perhaps as a reflection of small sample size. However, there did not appear to be an appreciable decrease in biting activity during the unusually rainy dry season.

The diurnal resting sites of L. trapidoi in a Panamanian forest have been identified by Chaniotis et al.

(1972). Although leaf litter on the forest floor was the preferred resting site, this species was also found to rest on green plants and tree trunks. The latter resting site was apparently seldom used in the Providencia study area (Table II-36).

L. trapidoi has been studied quite extensively in Panama. Tesh et al. (1971 and 1972) showed by the precipitin test that this species feeds on a broad range of mammals and indicate that host selection is influenced by availability. L. trapidoi also is known to feed on birds (Thatcher and Hertig 1966 and Tesh et al. 1971). Johnson and Hertig (1961) reared L. trapidoi and determined the duration of its various developmental stages. Chaniotis (1975) described a different technique for rearing this species and reported on several aspects of its behavior in the laboratory. Chaniotis (1974a) also studied the sugar-feeding behavior of L. trapidoi in the laboratory. The sites of larval development have been investigated by Hanson (1961) and Rutledge and Ellenwood (1975a, 1975b, 1975c).

L. trapidoi has been strongly implicated as a vector of cutaneous leishmaniasis (Johnson et al. 1962 and McConnell 1963), and in addition, a number of arboviruses have been isolated from this species (Tesh et al. 1974). Johnson et al. (1962) and McConnell (1963) have isolated leptomonad flagellates from wild-caught L. trapidoi which were subsequently shown to cause infections in the nose of

hamsters similar to those produced by Leishmania braziliensis sensu lato. Johnson et al. (1963) obtained infection rates of promastigotes (leptomonads) as high as 15.4% for females of L. trapidoi, but with very few exceptions (McConnell 1963) they were not conclusively shown to be Leishmania.

L. yuilli Young and Porter, 1972

L. yuilli appears to be near the northern limits of its range in the Providencia study area. This species has not been taken in Panama or any of the other Central American countries but has been found in Pará State, Brazil (Lewis 1975) and Ecuador (D. G. Young, personal communication). In Colombia the species has also been collected near Caucasia, Department of Antioquia and Tres Esquinas, Department of Caquetá (D. G. Young, personal communication).

L. yuilli was observed to be primarily a forest species. The modified geometric mean catch of this species for the Buenos Aires forest was almost three times as large as the corresponding mean catch for the Tiroteos forest which had been subjected to some selective cutting. For all levels combined a highly significant difference was detected in the biting activity of L. yuilli between the Buenos Aires site and each of the other two forest sites (Table II-18). The difference between the Buenos Aires and Providencia sites was due to the very reduced biting activity in the

understory and on the forest floor at the Providencia site, while the difference between the Buenos Aires and Tiroteos sites was primarily the result of diminished biting activity in the canopy at the Tiroteos site. In the clearing the biting activity of L. yuilli was greatest at site E (Table II-22) which was located at the edge of early secondary forest and pasture. This species was taken in smaller numbers at sites D (edge of mature forest and pasture) and F (edge of pioneer vegetation and pasture) and was seldom encountered at site C (open pasture) and sites A and B which were over 200 m from mature forest. The large number of specimens taken at site E is primarily the result of a very large catch at this site in March. A total of 29 individuals of L. yuilli were taken at this site during the remaining five catches whereas 39 were taken at site D. Thus in the clearing habitat the biting activity of L. yuilli was concentrated at the forest margin. Some biting also occurred in the pioneer vegetation which extended from the forest; however, this species appeared reluctant to extend very far into the clearing, even along the pioneer vegetation.

For the three forest sites combined, a highly significant difference was detected in the man-biting activity of L. yuilli between the canopy and each of the other two levels (Table II-7). However, the vertical stratification of this species' biting activity appeared to be particularly

influenced by forest structure. At the Providencia site where the upper canopy was quite dense, the biting activity of L. yuilli occurred primarily in the canopy (Table II-9) while in the relatively open Tiroteos forest, a significant difference was not detected between any of the levels (Table II-8).

Although the summary temporal pattern of biting activity for L. yuilli for the forest catches appears to be somewhat bimodal (Fig. II-14), the patterns for the individual nights were quite variable. On many of the nights there was a sudden, pronounced surge in biting activity during one or occasionally two catch periods, and these surges tended to be quite variable with respect to time (Fig. II-21). The biting activity of L. yuilli at the clearing sites tended to be concentrated between 0800 and 2200 hours (Fig. II-14).

L. yuilli was taken in the forest man-biting catches throughout the entire year. Seasonal variations in its biting activity are difficult to determine from this study, although there is an indication that its biting activity may have increased during February, March, and April. February and March are the last two months of the dry season. Adults of L. yuilli did not use the base of large trees as a diurnal resting site.

W. rotundipennis Fairchild and Hertig, 1951

W. rotundipennis has been found in Costa Rica, Panama, and Colombia (Fairchild and Hertig 1959, and Young 1971) at elevations ranging from 35 m (Young 1971) to 690 m.

The man-biting activity of W. rotundipennis was greatest in the clearing habitat where it was taken in rather similar magnitudes at both exposed and edge locations. The modified geometric mean catch for the clearing habitat was considerably larger than that for the forest (Table II-5). As mentioned earlier, comparisons between the forest and clearing series of catches should be made with caution, especially since the clearing catches were only made over a 6-month period. No statistically significant differences were detected in the biting activity of W. rotundipennis between the six clearing sites (Table II-23).

In the forest catches, W. rotundipennis was taken primarily at the Providencia site (Table II-20), but even at this site it was not numerous. The modified geometric mean catches for the three vertical levels at the Providencia platform site (Table II-11) were to varying degrees less than those for the clearing sites with the exception of site A (Table II-22).

No significant difference was detected in the man-biting activity of W. rotundipennis between the three vertical levels at the Providencia platform site (Table II-8).

W. rotundipennis was the only species regularly taken at the Providencia site which did not have a strong preference for the canopy at this location. The canopy preference was so pronounced in the other species that W. rotundipennis was the second most frequently encountered species on the forest floor at this site.

At the clearing sites the man-biting activity of W. rotundipennis tended to be concentrated between 1900 and 2400 hours (Fig. II-25). The temporal distribution of those individuals of this species taken in the forest catches is given in Table II-32. There was very little biting activity in the forest before 2000 hours. Adults of W. rotundipennis were present throughout the year; however, there was an insufficient number of catches to ascertain seasonal trends.

BIBLIOGRAPHY

- Allee, W. C. 1926. Measurement of environmental factors in the tropical rain-forest of Panama. *Ecology* 7: 273-302.
- Allen, L. H., Jr., E. Lemon, and L. Müller. 1972. Environment of a Costa Rican forest. *Ibid.* 53: 102-11.
- Allen, T. F. H. and S. Skagen. 1973. Multivariate geometry as an approach to algal community analysis. *Br. Phycol. J.* 8: 267-87.
- Anderson, A. J. B. 1971. Ordination methods in ecology. *J. Ecol.* 59: 713-26.
- Anonymous. 1969. Monografía del Departamento de Antioquia. Instituto Geográfico "Agustín Codazzi" Oficina de Estudios Geográficos. Bogotá. 98 pp.
- Barreto, P. 1969. Artrópodos haematófagos del Río Raposo, Valle, Colombia. IV. Psychodidae. *Caldasia* 10 (49): 459-72.
- Beals, E. 1960. Forest bird communities in the Apostle Islands of Wisconsin. *Wilson Bull.* 72: 156-81.
- Beals, E. W. 1973. Ordination: mathematical elegance and ecological naïveté. *J. Ecol.* 61: 23-35.
- Biagi F., F. and A. M. de B. de Biagi. 1953. Datos ecológicos de algunos flebotomus Mexicanos (Diptera, Psych.). *An. Inst. Biol. Univ. Nac. Auton. Mex.* 24: 445-50.
- Bram, R. A. 1967. Classification of Culex subgenus Culex in the New World (Diptera: Culicidae). *Proc. U. S. Natl. Mus.* 120(3557): 1-122.
- Bray, J. R. and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.* 27: 325-49.

Budowski, G. 1963. Forest succession in tropical lowlands. *Turrialba* 13: 42-44.

1965. Distribution of tropical American rain forest species in the light of successional processes. *Ibid.* 15: 40-42.

Chaniotis, B. N. 1974a. Sugar-feeding behavior of *Lutzomyia trapidoi* (Diptera: Psychodidae) under experimental conditions. *J. Med. Entomol.* 11: 73-79.

1974b. Use of external characters for rapid identification of phlebotomine sandflies in vector studies. *Ibid.* 11: 501.

1975. A new method for rearing *Lutzomyia trapidoi* (Diptera: Psychodidae), with observations on its development and behavior in the laboratory. *Ibid.* 12: 183-88.

Chaniotis, B. N. and M. A. Correa. 1974. Comparative flying and biting activity of Panamanian phlebotomine sandflies in a mature forest and adjacent open space. *Ibid.* 11: 115-16.

Chaniotis, B. N., M. A. Correa, R. B. Tesh, and K. M. Johnson. 1971b. Daily and seasonal man-biting activity of phlebotomine sandflies in Panama. *Ibid.* 8: 415-20.

1974. Horizontal and vertical movements of phlebotomine sandflies in a Panamanian rain forest. *Ibid.* 11: 369-75.

Chaniotis, B. N., J. M. Neely, M. A. Correa, R. B. Tesh, and K. M. Johnson. 1971a. Natural population dynamics of phlebotomine sandflies in Panama. *Ibid.* 8: 339-52.

Chaniotis, B. N., R. B. Tesh, M. A. Correa, and K. M. Johnson. 1972. Diurnal resting sites of phlebotomine sandflies in a Panamanian tropical forest. *Ibid.* 9: 91-98.

Christensen, H. A. 1972. Check list of the phlebotomine sand flies (Diptera: Psychodidae) of Panama including two species not previously reported. *Mosq. News* 32: 88-89.

- Christensen, H. A. and G. B. Fairchild. 1971. Lutzomyia tintinnabula n. sp. (Diptera: Psychodidae) from Panama. J. Med. Entomol. 8: 301-3.
- Christensen, H. A., A. Herrero, and S. R. Telford, Jr. 1969. Leishmania braziliensis s. lat., isolated from Lutzomyia panamensis in Panama. J. Parasitol. 55: 1090-91.
1972. Enzootic cutaneous leishmaniasis in eastern Panama II: entomological investigations. Ann. Trop. Med. Parasitol. 66: 55-66.
- Colless, D. H. 1957. Components of the catch curve of Culex annulus in Singapore. Nature (Lond.) 180: 1496-97.
- Dalmat, H. T. 1955. The black flies (Diptera: Simuliidae) of Guatemala and their role as vectors of onchocerciasis. Smithsonian Misc. Collect. 125: i-vii, 1-425.
- Disney, R. H. L. 1968. Observations on a zoonosis: leishmaniasis in British Honduras. J. Appl. Ecol. 5: 1-59.
- Downes, J. A. 1971. The ecology of blood-sucking Diptera: An evolutionary perspective. In Ecology and Physiology of Parasites, A. M. Fallis, ed. Univ. of Toronto Press. 232-58.
- Fairchild, G. B. and M. Hertig. 1948. Notes on the Phlebotomus of Panama (Diptera, Psychodidae). III. P. cruciatus Coq., trinidadensis Newst. and gomezi Nitz. Ann. Entomol. Soc. Am. 41: 247-57.
1951. Notes on the Phlebotomus of Panama (Diptera, Psychodidae). VII. The subgenus Shannonomyia Pratt. Ibid. 44: 399-421.
1952. Notes on the Phlebotomus of Panama. IX. Descriptions of seven new species. Ibid. 45: 505-28.
1957. Notes on the Phlebotomus of Panama. XIII. The vexator group, with descriptions of new species from Panama and California. Ibid. 50: 325-34.
1959. Geographic distribution of the Phlebotomus sandflies of Central America (Diptera: Psychodidae). Ibid. 52: 121-24.

- Forattini, O. P. 1957. Culicoides da região Neotropical (Diptera, Ceratopogonidae). Arq. Fac. Hig. Saúde Publica Univ. São Paulo 11(2): 159-526.
- Galindo, P., H. Trapidoi, and S. J. Carpenter. 1950. Observations on diurnal forest mosquitoes in relation to sylvan yellow fever in Panama. Am. J. Trop. Med. 30: 533-74.
- Gillies, M. T. 1972. Some aspects of mosquito behaviour in relation to the transmission of parasites. In Behavioural Aspects of Parasite Transmission, E. U. Canning and C. A. Wright, eds. Acad. Press, London. 69-81.
- Grubb, P. J., J. R. Lloyd, T. D. Pennington, and T. C. Whitmore. 1963. A comparison of montane and lowland rain forest in Ecuador. I. The forest structure, physiognomy, and floristics. J. Ecol. 51: 567-601.
- Grubb, P. J. and T. C. Whitmore. 1966. A comparison of montane and lowland rain forest in Ecuador. II. The climate and its effects on the distribution and physiognomy of the forests. Ibid. 54: 303-34.
- Haddow, A. J. 1945. The mosquitoes of Bwamba County, Uganda. II. Biting activity with special reference to the influence of microclimate. Bull. Entomol. Res. 36: 33-73.
1954. Studies of the biting-habits of African mosquitos. An appraisal of methods employed, with special reference to the twenty-four-hour catch. Ibid. 45: 199-242.
1960. Studies on the biting habits and medical importance of East African mosquitos in the genus Aedes. I.-Subgenera Aedimorphus, Banksinella and Dunnius. Ibid. 50: 759-79.
- 1961a. Studies on the biting habits and medical importance of East African mosquitos in the genus Aedes. II.-Subgenera Mucidus, Diceromyia, Finlaya and Stegomyia. Ibid. 52: 317-51.
- 1961b. Entomological studies from a high tower in Mpanga forest, Uganda. VII. The biting behaviour of mosquitos and tabanids. Trans. R. Entomol. Soc. Lond. 113: 315-35.

- Haddow, A. J. and P. S. Corbet. 1961. Entomological studies from a high tower in Mpanga Forest, Uganda. II. Observations on certain environmental factors at different levels. Ibid. 113: 257-69.
- Haddow, A. J., J. D. Gillett, and R. B. Highton. 1947. The mosquitoes of Bwamba County, Uganda. V.-The vertical distribution and biting-cycle of mosquitoes in rain-forest, with observations on microclimate. Bull. Entomol. Res. 37: 301-30.
- Haddow, A. J. and Y. Ssenkubuge. 1973. The mosquitoes of Bwamba County, Uganda. IX. Further studies on the biting behaviour of an outdoor population of the Anopheles gambiae Giles complex. Ibid. 62: 407-14.
- Hanson, W. J. 1961. The breeding places of Phlebotomus in Panama (Diptera, Psychodidae). Ann. Entomol. Soc. Am. 54: 317-22.
- Holdridge, L. R. 1947. Determination of world plant formations from simple climatic data. Science (Wash. DC) 105: 367-68.
- Holdridge, L. R., W. C. Grenke, W. H. Hatheway, T. Liang, and J. A. Tosi, Jr. 1971. Forest Environments in Tropical Life Zones. A Pilot Study. Pergamon Press, New York. 747 pp.
- Johnson, P. T. 1961. Autogeny in Panamanian Phlebotomus (Diptera: Psychodidae). Ann. Entomol. Soc. Am. 54: 116-18.
- Johnson, P. T. and M. Hertig. 1961. The rearing of Phlebotomus sandflies (Diptera: Psychodidae). II. Development and behavior of Panamanian sandflies in laboratory culture. Ibid. 54:764-76.
- Johnson, P. T., E. McConnell, and M. Hertig. 1962. Natural and experimental infections of leptomonad flagellates in Panamanian Phlebotomus sandflies. J. Parasitol. 48: 158.
1963. Natural infections of leptomonad flagellates in Panamanian Phlebotomus sandflies. Exp. Parasitol. 14: 107-22.
- Kettle, D. S. 1969. The biting habits of Culicoides furens (Poey) and C. barbosa Wirth & Blanton. I. The 24-h cycle, with a note on differences between collectors. Bull. Entomol. Res. (1968) 59: 21-31.

- Kettle, D. S. and J. R. Linley. 1967. The biting habits of Leptoconops bequaerti. II. Effect of meteorological conditions on biting activity; 24 hour and seasonal cycles. J. Appl. Ecol. 4: 397-420.
- Kruijf, H. A. M. de. 1972. Aspects of the ecology of mosquitoes in Surinam. Stud. Fauna Suriname other Guyanas XIII 51: 1-56.
- Lane, J. 1953. Neotropical Culicidae. Vol. I. Univ. São Paulo. São Paulo, Brazil. 548 pp.
- Lewis, D. J. 1971. Phlebotomid sandflies. Bull. W. H. O. 44: 535-51.
1974. The biology of Phlebotomidae in relation to leishmaniasis. Annu. Rev. Entomol. 19: 363-84.
- 1975a. The Lutzomyia flaviscutellata complex (Diptera: Psychodidae). J. Med. Entomol. 12: 363-68.
- 1975b. Functional morphology of the mouth parts in New World phlebotomine sandflies. Trans. R. Entomol. Soc. Lond. 126: 497-532.
- Llanos, B. 1973. Flebótomos de la selva Peruana (Diptera: Psychodidae). Rev. Peru. Entomol. 16: 29-50.
- Lumsden, W. H. R. 1952. The crepuscular biting activity of insects in the forest canopy in Bwamba, Uganda. A study in relation to the sylvan epidemiology of yellow fever. Bull. Entomol. Res. 42: 721-60.
- Martins, A. V., A. L. Falcão, and J. E. Silva. 1963. Notas sobre os flebótomos do Território de Roraima, com a descrição de três novas espécies (Diptera, Psychodidae). Rev. Bras. Biol. 23: 333-48.
- Martins, A. V. and E. N. Morales-Farias. 1972. Sobre a distribuição geográfica dos flebotomíneos americanos (Diptera, Psychodidae, Phlebotominae). Ibid. 32: 361-71.
- McConnell, E. 1963. Leptomonads of wild-caught Panamanian Phlebotomus: culture and animal inoculation. Exp. Parasitol. 14: 123-28.
- Miller, R. G., Jr. 1966. Simultaneous Statistical Inference. McGraw-Hill Book Co., New York. 272 pp.

- Mirsa, A. 1952. El desarrollo de Phlebotomus panamensis Shannon, 1926 y Ph. gomezi Nitzulescu (*) 1931 (Diptera, Psychodidae) en condiciones de laboratorio. Rev. Sanid. Asist. Soc. 16: 561-72.
- Morales-Alarcón, A., F. de Osorno, and E. Osorno-Mesa. 1974. Phlebotominae de Colombia. X. Descripción de la hembra de Lutzomyia dendrophila (Mangabeira, 1942) y del macho y la hembra de Lutzomyia disiuncta sp. n. (Diptera, Psychodidae). Rev. Bras. Biol. 34: 443-52.
- Nemenyi, P. 1962. t tests for comparing more than two means. J. Indian Med. Prof. 9: 4298-309.
1968. Linear hypotheses: multiple comparisons. In International Encyclopedia of Social Sciences. The Macmillan Co. & The Free Press, New York. 337-51.
- Odum, E. P. 1971. Fundamentals of Ecology, 3rd ed. W. B. Saunders Co., Philadelphia, PA. 574 pp.
- Orloci, L. 1966. Geometric models in ecology. I. The theory and application of some ordination methods. J. Ecol. 54: 193-215.
- Ortiz, I. and J. V. Scorza. 1963. Notas biológicas y taxonómicas sobre algunos Phlebotominae (Diptera, Psychodidae) de Rancho Grande, Venezuela. Acta Biol. Venez. 3(23): 341-61.
- Osorno, F. de, E. Osorno-Mesa, and A. Morales-Alarcón. 1972b. Phlebotominae de Colombia (Diptera, Psychodidae). VII. Descripción de Lutzomyia andina sp. n. y Lutzomyia quasitownsendi sp. n. Bol. Mus. Hist. Nat. U. F. M. G. (Univ. Fed. de Minas Gerais) Zool. 12: 1-29.
- Osorno-Mesa, E., A. Morales-Alarcón, and F. de Osorno. 1967. Phlebotominae de Colombia (Diptera, Psychodidae). I. Distribución geográfica de especies de Phlebotomus registradas con algunas anotaciones biológicas y descripción de una nueva. Caldasia 10 (46): 27-38.
- Osorno-Mesa, E., A. Morales-Alarcón, F. de Osorno, and C. Ferro-Vela. 1972a. Phlebotominae de Colombia. IX. Distribución geográfica de especies de Brumptomyia Franca y Parrot, 1921 y Lutzomyia Franca, 1924 encontradas en Colombia S. A. Separata de la Rev. Acad. Colomb. Cienc. Exactas Fis. Nat. 14(53). 81 pp.

- Osorno-Mesa, E., A. Morales-Alarcón, F. de Osorno, and P. Muñoz de Hoyos. 1970. Phlebotominae de Colombia (Diptera, Psychodidae). VI. Descripción de Lutzomyia longiflocosa n. sp. y Lutzomyia bifoliata n. sp. Bol. Mus. Hist. Nat. U. F. M. G. (Univ. Fed. de Minas Gerais) Zool. 6: 1-22.
- Pielou, E. C. 1969. An Introduction to Mathematical Ecology. Wiley-Interscience, New York. 286 pp.
- Pifano C., F. 1940. Sobre el desarrollo de Leishmania brasiliensis en Phlebotomus de Venezuela. Gac. Med. (Caracas) 48: 414-16.
- Pifano C., F., I. Ortiz, and A. Alvarez. 1960. La ecología, en condiciones naturales y de laboratorio, de algunas especies de Phlebotomus de la region de Guatopo, Estado Miranda, Venezuela. Arch. Venez. Med. Trop. Parasitol. Med. 3: 63-71.
- Richards, P. W. 1952. The Tropical Rain Forest. An Ecological Study. Cambridge University Press, London. 450 pp.
- Rohdendorf, B. 1974. The Historical Development of Diptera. Univ. of Alberta Press, Edmonton, Alberta. 360 pp. (translation of original Russian language edition published by "Nauka" as volume 100, Transactions of the Institute of Paleontology, Academy of Sciences of the USSR, Moscow, 1964).
- Rutledge, L. C. and D. A. Ellenwood. 1975a. Production of phlebotomine sandflies on the open forest floor in Panama: the species complement. Environ. Entomol. 4: 71-77.
- 1975b. Production of phlebotomine sandflies on the open forest floor in Panama: hydrologic and physiographic relations. Ibid. 4: 78-82.
- 1975c. Production of phlebotomine sandflies on the open forest floor in Panama: phytologic and edaphic relations. Ibid. 4: 83-89.
- Rutledge, L. C., D. A. Ellenwood, and L. Johnston. 1975. An analysis of sand fly light trap collections in the Panama Canal Zone (Diptera:Psychodidae). J. Med. Entomol. 12: 179-83.

- Schneider, C. R. and M. Hertig. 1966. Immunodiffusion reactions of Panamanian Leishmania. Exp. Parasitol. 18: 25-34.
- Scorza, J. V., I. McLure, and M. T. de McLure. 1968a. Observaciones biológicas sobre algunos flebotomos de "Rancho Grande" (Venezuela). 7. Notas sobre relaciones biométricas entre algunos Phlebotomus (Diptera, Psychodidae) con antropofilia facultativa y otros con antropofilia accidental. Acta Biol. Venez. 6: 87-96.
- Scorza, J. V., I. Ortiz, and I. Gomez. 1968b. Observaciones biológicas sobre algunos flebotomos de "Rancho Grande" (Venezuela). 8. Sobre la fluctuación estacional de los microhabitats. Ibid. 6: 97-104.
- Scorza, J. V., I. Ortiz, and M. T. de McLure. 1963. Ecología de las formas estacionales de Phlebotomus townsendi Ortiz, 1960 y Phlebotomus cayennensis Floch & Abonnenc, 1941 (Diptera, Psychodidae) en el centro-norte de Venezuela. Ibid. 3: 437-53.
- Shaw, J. J. and R. Lainson. 1968. Leishmaniasis in Brazil: II. Observations on enzootic rodent leishmaniasis in the lower Amazon region--The feeding habits of the vector, Lutzomyia flaviscutellata in reference to man, rodents and other animals. Trans. R. Soc. Trop. Med. Hyg. 62: 396-405.
- Shaw, J. J., R. Lainson, and R. D. Ward. 1972. Leishmaniasis in Brazil: VII. Further observations on the feeding habits of Lutzomyia flaviscutellata (Mangabeira) with particular reference to its biting habits at different heights. Ibid. 66: 718-23.
- Sheldon, A. L. 1969. Equitability indices: dependence on the species count. Ecology 50: 466-67.
- Sherlock, I. A. and N. Guitton. 1969. Observações sobre calazar em Jacobina, Bahia. IV--Variação horária e estacional do Phlebotomus longipalpis. Rev. Bras. Malariol. Doencas Trop. 2: 715-27.
- Snedecor, G. W. and W. G. Cochran. 1967. Statistical Methods. Iowa State University Press, Ames, Iowa. 593 pp.

- Steel, R. G. D. and J. H. Torrie. 1960. Principles and Procedures of Statistics. McGraw-Hill Book Co., Inc., New York. 481 pp.
- Tesh, R. B. and B. N. Chaniotis. 1975. Transovarial transmission of viruses by phlebotomine sandflies. In Pathobiology of Invertebrate Vectors of Disease, L. A. Bulla, Jr. and T. C. Cheng, eds. Ann. N. Y. Acad. Sci. 266: 125-34.
- Tesh, R. B., B. N. Chaniotis, M. D. Aronson, and K. M. Johnson. 1971. Natural host preferences of Panamanian phlebotomine sandflies as determined by precipitin test. Am. J. Trop. Med. Hyg. 20: 150-56.
- Tesh, R. B., B. N. Chaniotis, B. R. Carrera, and K. M. Johnson. 1972. Further studies on the natural host preferences of Panamanian phlebotomine sandflies. Am. J. Epidemiol. 95: 88-93.
- Tesh, R. B., B. N. Chaniotis, P. H. Peralta, and K. M. Johnson. 1974. Ecology of viruses isolated from Panamanian phlebotomine sandflies. Am. J. Trop. Med. Hyg. 23: 258-69.
- Thatcher, V. E. 1968. Studies of phlebotomine sandflies using castor oil traps baited with Panamanian animals. J. Med. Entomol. 5: 293-97.
- Thatcher, V. E. and M. Hertig. 1966. Field studies on the feeding habits and diurnal shelters of some Phlebotomus sandflies (Diptera:Psychodidae) in Panama. Ann. Entomol. Soc. Am. 59: 46-52.
- Trapido, H. and P. Galindo. 1957. Mosquitoes associated with sylvan yellow fever near Almirante, Panama. Am. J. Trop. Med. Hyg. 6: 114-44.
- Ward, R. D., J. J. Shaw, R. Lainson, and H. Fraiha. 1973. Leishmaniasis in Brazil: VIII. Observations on the phlebotomine fauna of an area highly endemic for cutaneous leishmaniasis, in the Serra dos Carajás, Pará State. Trans. R. Soc. Trop. Med. Hyg. 67: 174-83.
- Wijers, D. J. B. and R. Linger. 1966. Man-biting sandflies in Surinam (Dutch Guiana): Phlebotomus anduzei as a possible vector of Leishmania braziliensis. Ann. Trop. Med. Parasitol. 60: 501-8.

- Wilcoxon, F. and R. A. Wilcox. 1964. Some Rapid Approximate Statistical Procedures. Lederle Laboratories, Pearl River, New York. 59 pp.
- Williams, C. B. 1937. The use of logarithms in the interpretation of certain entomological problems. *Ann. Appl. Biol.* 24: 404-14.
1939. An analysis of four years' captures of insects in a light trap. Part I. General survey; sex proportion; phenology; and time of flight. *Trans. R. Entomol. Soc. Lond.* 89: 79-131.
1951. Comparing the efficiency of insect traps. *Bull. Entomol. Res.* 42: 513-17.
- Williams, P. 1965. Observations on the phlebotomine sandflies of British Honduras. *Ann. Trop. Med. Parasitol.* 59: 393-404.
1966. The biting rhythms of some anthropophilic phlebotomine sandflies in British Honduras. *Ibid.* 60: 357-64.
- 1970a. On the vertical distribution of Phlebotomine sandflies (Dipt., Psychodidae) in British Honduras (Belize). *Bull. Entomol. Res.* (1968) 59: 637-46.
- 1970b. Phlebotomine sandflies and leishmaniasis in British Honduras (Belize). *Trans. R. Soc. Trop. Med. Hyg.* 64: 317-64.
- Young, D. G. 1971. The phlebotomine sand flies of Colombia (Diptera, Psychodidae). MS thesis. University of Florida. 251 pp.
1973. Two new phlebotomine sand flies from Colombia (Diptera: Psychodidae). *Fla. Entomol.* 56: 106-12.
- Young, D. G. and C. H. Porter. 1972. Lutzomyia yuilli, a new man-biting phlebotomine sand fly from Colombia (Diptera: Psychodidae). *J. Med. Entomol.* 9: 524-26.
1974. Lutzomyia cirrita n. sp. from Colombia with a new synonym in the genus (Diptera: Psychodidae: Phlebotominae). *Fla. Entomol.* 57: 321-25.

APPENDIX A

Additional Historical Information about the
Providencia Region

Although Zarogoza was an early center of Spanish gold mining, this activity eventually decreased in the region, and in the eighteenth century Zarogoza became a poor river village. At the time of its settlement, an estimated 2,000 Indian families lived in the Zarogoza region.¹ The extent of early Indian settlement near Providencia is unknown but at least some is thought to have occurred. There is no evidence that any of the early Spanish settled in the hilly Providencia region, and the rapid, boulder strewn Río Anorí is unnavigable. The first known land acquisition in the Providencia region occurred in 1886 for a tract of land near La Tirana (Fig. II-1).

Increased gold mining activity at the beginning of the twentieth century on the lower Nechi and its tributary the Río Anorí prompted the construction of a road from Dos Bocas, at the confluence of the Río Porce and the Río Nechi, south-

¹James J. Parsons, Antioqueno Colonization in Western Colombia, rev. ed. (Berkeley and Los Angeles, 1968), p. 44.

ward to the town of Anorí. This road, for the most part, follows the Río Nechi upstream to where it meets the Río Anorí and then follows the latter to Anorí. However, frequent mud slides have now reduced this road to a mule trail with the exception of the portion from Dos Bocas to Providencia and Los Aljibes which is maintained by Pato Consolidated Gold Dredging, Ltd.

In 1922 the Compania Colombia Corporation, Ltd., now Pato Consolidated Gold Dredging, Ltd., purchased Dos Bocas from the French Company which initiated hydraulic mining on the lower Nechi in 1909. Large tracts of the lower Río Anorí watershed were purchased in 1937 by the Compania Colombia Corporation, Ltd., with additional acquisitions being made through 1940. The hydroelectric plant at Providencia, including its substation at Los Aljibes, was constructed in the early 1940's and supplies the majority of the electricity used by the dredges and camp at El Bagre.

Two small cacao plantations were the only agricultural endeavors in the region surrounding Providencia of greater magnitude than the subsistence type of farming common to the locality, and both had ceased operation a number of years prior to this study. The first was established in 1922 about 2 kilometers north of Providencia at La Toma and the second was begun in 1934 at Remolina.

APPENDIX B

Additional Characteristics of the Forest Vegetation

Variation in forest structure and floristics may account for considerable local differences in the composition of haematophagous Diptera populations in the Neotropics. For example, Rutledge and Ellenwood¹ have found that the site of larval development for certain species of phlebotomine sandflies may be related to large trees and lianas which have a distinctive effect on the forest soil and litter. To provide a more detailed description of the forests of the Providencia region and to determine whether the marked differences in the man-biting activity of Diptera between the Buenos Aires 1 and Tiroteos platform sites could be related to variations in forest structure, the following analyses of the vegetation were made.

A 1.5 hectare area of forest surrounding the Buenos Aires 1 platform sites was intensively studied by Dr. E. W. Beals of the University of Wisconsin-Madison Botany Department, and we are indebted to him for allowing us to use a

¹L. C. Rutledge and D. A. Ellenwood. 1975. Production of phlebotomine sandflies on the open forest floor in Panama: phytologic and edaphic relations. Environ. Entomol. 4: 83-89.

portion of these unpublished data. Diameter at breast height (dbh), or above taller buttresses, was recorded for each tree (10 cm dbh or over) and sapling (2.5-10 cm dbh). At the Buenos Aires site each tree and sapling was mapped by triangulation from stakes 10 m apart. This method was also used to estimate their height. The presence of epiphytes and lianas was recorded, although those epiphytes less than 0.5 m in diameter located in the crown of the canopy trees were not readily visible and hence were frequently overlooked. A map of all trees and saplings occurring in a 592 m² portion of the 1.5 hectare area sampled was constructed, and a grid of 3.05 x 3.05 m square quadrats was superimposed over the map to permit a comparison of the pattern of the trees and saplings to a Poisson distribution.

At the Tiroteos location a map was constructed of all the trees and saplings in a 242 m² area surrounding the platform site using a grid of 3.05 x 3.05 m square contiguous quadrats. The tree heights were estimated with the two platforms serving as reference points. An experienced native helped with distinguishing the species of trees and saplings. A comparison of selected characteristics of the two forests is presented in Tables II-B1 to II-B5.

At both the Buenos Aires and Tiroteos sites an upper closed canopy was formed by trees 22 to 30 m tall, but a

few scattered emergents extended to 35 m. The few measurements of tree height made at the Providencia site indicated that the upper canopy of this forest was about 5 to 10 m taller than that of the other two forests. The height distribution of the trees and saplings (Table II-B1) does not indicate the presence of distinct tree strata in either the Buenos Aires or the Tiroteos forests. The reduced number of individuals under 10 m in the Buenos Aires forest reveals the selective removal of some 5 to 8 cm dbh saplings for construction of the platform sites. No selective cutting of saplings occurred at the Tiroteos site, and the difference in sapling density between the two sites is apparent from the diameter class densities given in Table II-B2.

Palms were most abundant in the Tiroteos forest where, with an estimated density of 1,529/ha., they were a conspicuous component of the understory. With the exception of a couple of 20 m high Attalea amygdalina at the Tiroteos study site, the palms at both this and the Buenos Aires site were under 10 m in height. Although buttresses occurred on 30% of the trees at the Buenos Aires site and 21% at the Tiroteos site, they were generally small and inconspicuous. Buttressing was much more evident in the Providencia forest where Carapa guianensis Aubl., a tree frequently possessing immense buttresses, was the dominant canopy species. Stilt roots were scarce, occurring on less than 10% of the trees and saplings at the two forest sites

Table II-B1
Height distribution of trees and saplings.^a

Site	0-5 m	5-10 m	10-15 m	15-20 m	20-25 m	25-30 m	30-35 m
Buenos Aires	16	14	16	14	13	1	1
Tiroteos ^b	27	13	6	3	3	4	

^aNumber of individuals in 592 m² at the Buenos Aires site and 242 m² at the Tiroteos site.

^bA 5.3 dbh "mortinu" cut by natives is not included.

Table II-B2
Summary of vegetation data by height and diameter class.

	Buenos Aires			Tiroteos	
	Mean height (m)	Density (No./m ²)	Percent of population with:	Mean height (m)	Density (No./m ²)
			Epiphytes and vines		
Height class (m)					
Above 35		0.000			0.000
13-35	19.9	0.059	88 69	21.1	0.054
5-13	9.6	0.050	44 41	7.7	0.066

Diameter class (cm)					
Over 60	24.1	0.006	100 100	27.4	0.004
30-60	20.6	0.015	100 88	23.9	0.025
15-30	19.5	0.028	87 60	15.2	0.029
7.5-15	12.1	0.046	54 50	10.5	0.033
2.5-7.5	--	0.044	-- --	4.5	0.145

sampled. Tree ferns did not occur on the sample plots and generally appeared to be limited to areas bordering streams.

Herbaceous epiphytes and lianas were abundant on the upper and middle strata trees at the Buenos Aires study site (Table II-B3). Bromeliads and Araceae were the predominant herbaceous epiphytic forms but ferns, orchids, and cyclanths were also common. Aroids were the dominant type on trunks while bromeliads were the most numerous component of the crowns. The distribution of tank epiphytes was quite localized with 39% of them occurring on 2 of the 44 trees in the sample plot. Both of these trees were Caryocar costaricense Donn. Sm. and were the ones in which the platforms were constructed. Many of the other herbaceous epiphytes tended to have similarly aggregated patterns, e.g., nearly half of the canopy aroids were located in one of the C. costaricense trees. Comparatively few tank epiphytes were present at the Tiroteos study site. Lianas and vines had an estimated density of 1,651 stems/ha. at the Buenos Aires site.

Epiphytic mosses and lichens were common on tree trunks. At the Buenos Aires study site moss cover averaged about 30% but varied from 0 to 85%. Lichens were more abundant with a mean coverage of about 50% and a range from 1 to 95%.

Ground cover in all three forests was sparse and consisted primarily of occasional ferns, herbaceous dicots,

Table II-B3
Herbaceous epiphytes observed at the Buenos Aires site.^a

	Tank epiphytes	Ferns	Araceae	Orchids	Cyclanthaceae	Other monocots	Dicots
Trunk	27	20	45	7	6	1	12
Canopy	63	16	41	15	16	1	9
Total	90	36	86	22	22	2	21

^aOccurring on trees within the 592 m² sample plot.

seedlings, and cyclanths. On some of the steep slopes in the Buenos Aires forest where light penetrated to the forest floor, scattered Araceae and Marantaceae were also present. Luxuriant growths of Selaginella often occurred along the paths just within the forests, but this plant became less abundant and gradually disappeared as one went further into the forests.

The tree pattern at the Buenos Aires and Tiroteos sites was compared with the Poisson distribution (Table II-B4). The occurrence of an aggregated pattern should indicate the presence of openings which could be expected to have the effect of lowering the humidity within a forest. Humidity is known to have an influence on the distribution of mosquitoes in a tropical forest environment (Pittendrigh).² It would have been interesting to relate insect distribution to humidity differences within the forests as determined from the simultaneous use of hydrothermographs positioned at both ground level and in the canopy of each of the platform sites, but unfortunately this was not possible. The pattern of trees plus saplings was also compared with the Poisson distribution for both sites (Table II-B5).

The variance over mean ratio for trees (Table II-B4) is less than one for both forest sites which suggests a

²C. S. Pittendrigh. 1950. The ecoclimatic divergence of Anopheles bellator and A. homunculus. Evolution 4: 43-63.

Table II-B4
Tree pattern compared with Poisson distribution.

Site	Quadrats	Trees ^a	\bar{x}	s^2	$\frac{s^2}{\bar{x}}$	χ^2	df	t	df
Buenos Aires	58	44	0.759	0.607	0.800	4.67	3	1.07	57
Tiroteos	26	19	0.731	0.445	0.609	3.13	3	1.38	25

^a dbh \geq 10 cm.

Table II-B5
Tree and sapling pattern compared with Poisson distribution.

Site	Quadrats	Trees ^a	Saplings ^b	\bar{x}	s^2	$\frac{s^2}{\bar{x}}$	χ^2	df	t	df
Buenos Aires	58	44	32	1.310	1.551	1.184	4.48	5	0.98	57
Tiroteos	26	19	38	2.192	2.322	1.059	8.66	6	0.21	25

^a dbh \geq 10 cm.

^b dbh \geq 2.5 cm, $<$ 10 cm.

somewhat regular spacing of trees and thus an absence of forest openings. However, the chi-square and t values (Greig-Smith)³ indicate the departures from a random pattern were not significant. The mean nearest neighbor distance between trees over 13 m tall was 2.05 m at the Buenos Aires sample plot and 2.20 m at the Tiroteos site. When trees and saplings are considered together (Table II-B5), the variance over mean ratio exceeds unity, although only slightly so at the Tiroteos site. The chi-square and t values are nonsignificant, once again indicating the departures from a random pattern were not significant. The small size of the areas sampled undoubtedly has an influence on the results, especially at the Tiroteos forest where the area surrounding the platform site seemed to have a greater density of large trees than other portions of the forest. In fact, openings in the upper canopy were apparent in some areas. The tests of departure from randomness are, of course, influenced by the size of the quadrat used.

³P. Greig-Smith. 1964. Quantitative Plant Ecology, 2nd ed. Butterworths, London. 256 pp.

APPENDIX C

Checklist of Phlebotomine Sandflies of the
Providencia Region^a

- Brumptomyia leopoldi* (Rodriguez) 1953
- Lutzomyia abbonenci* (Floch and Chassignet), 1947
- L. aclydifera* (Fairchild and Hertig), 1952
- L. aragaoi* (Costa Lima), 1932
- L. barretto* (Mangabeira), 1942
- L. bifoliata* Osorno-Mesa, Morales-Alarcon, de Osorno,
and Muñoz de Hoyos, 1970
- L. camposi* (Rodriguez), 1950
- L. caprina* Osorno-Mesa, Morales-Alarcon and Osorno, 1972
- L. carpenteri* (Fairchild and Hertig), 1953
- L. cirrita* Young and Porter, 1974
- L. dasymera* (Fairchild and Hertig), 1961
- L. gomezi* (Nitzulescu), 1931
- L. hartmanni* (Fairchild and Hertig), 1957
- L. micropyga* (Mangabeira), 1942
- L. nocticola* Young, 1973
- L. nordestina* (Mangabeira), 1942

^aBased on identifications made by D. G. Young, Department of Entomology, University of Florida.

- L. olmeca-bicolor Fairchild and Theodor, 1971
- L. orsonoi (Ristorcelli and Van Ty), 1941
- L. panamensis (Shannon), 1926
- L. pessoana (Barretto), 1955
- L. pilosa (Damasceno and Causey), 1944
- L. rorotaensis (Floch and Abonnenc), 1944
- L. runoides (Fairchild and Hertig), 1953
- L. saulensis (Floch and Abonnenc), 1944
- L. serrana (Damasceno and Arouck), 1949
- L. shannoni (Dyar), 1929
- L. spinosa (Floch and Abonnenc), 1942
- L. tintinnabula Christensen and Fairchild, 1971
- L. trapidoi (Fairchild and Hertig), 1952
- L. trinidadensis (Newstead), 1922
- L. triramula (Fairchild and Hertig), 1952
- L. tuberculata (Mangabeira), 1941
- L. vespertilionis (Fairchild and Hertig), 1947
- L. yuilli Young and Porter, 1972
- L. sp. N (verrucarum group)
- L. sp. N (ungrouped)
- Warileya rotundipennis Fairchild and Hertig, 1951

APPENDIX D

The 132 Catches Used in the Ordination Analyses^a

Habitat ^b	Month	Year ^c	Site ^d	Level ^e	<u>L. hartmanni</u>	<u>L. trapidoi</u>	<u>L. yuilli</u>	<u>L. panamensis</u>	<u>L. tintinnabula</u>	<u>L. bifoliata</u>	<u>L. gomezi</u>	<u>W. rotundipennis</u>
1	9	0	3	1	18	0	0	1	0	0	0	1
1	9	0	3	2	23	2	0	0	0	0	0	0
1	9	0	3	3	51	9	3	0	1	0	0	0
1	9	0	1	1	85	9	4	2	11	1	0	0
1	9	0	1	2	53	12	4	0	0	0	0	0
1	9	0	1	3	123	40	22	2	1	1	0	0
1	10	0	1	1	203	22	19	3	6	0	0	0
1	10	0	1	2	48	26	5	2	0	0	0	0
f 1	10	0	1	3	45	58	44	0	0	1	0	0
1	10	0	4	1	11	0	9	0	1	0	0	1
1	10	0	4	2	41	30	9	1	0	2	0	0
1	10	0	4	3	26	55	24	1	0	0	1	0
1	11	0	1	1	106	17	15	0	14	0	0	0
1	11	0	1	2	38	5	11	1	0	0	0	0
1	11	0	1	3	54	12	20	1	0	0	0	0
1	11	0	4	1	7	0	2	1	0	0	0	0
1	11	0	4	2	20	14	8	0	0	0	0	0
1	11	0	4	3	18	10	2	0	0	0	0	0
1	12	0	3	1	14	4	0	1	0	0	4	0
1	12	0	3	2	33	20	0	0	0	0	0	0

^b Habitat	Month	Year ^c	Site ^d	Level ^e	<u>L. hartmanni</u>	<u>L. trapidoi</u>	<u>L. yuilli</u>	<u>L. panamensis</u>	<u>L. tintinnabula</u>	<u>L. bifoliata</u>	<u>L. gomezi</u>	<u>W. rotundipennis</u>
1	12	0	3	3	21	20	0	0	0	5	1	0
1	12	0	1	1	211	26	6	3	10	0	0	0
1	12	0	1	2	38	15	2	1	0	0	0	0
1	12	0	1	3	99	70	18	3	0	0	0	0
1	1	1	4	1	11	1	2	0	0	0	0	0
1	1	1	4	2	27	10	0	4	0	2	0	0
1	1	1	4	3	21	13	2	3	0	2	0	0
1	1	1	1	1	79	3	0	0	6	0	0	0
1	1	1	1	2	16	1	1	0	0	0	0	0
1	1	1	1	3	62	16	14	0	0	0	0	0
1	1	1	3	1	27	5	0	0	0	0	0	4
1	1	1	3	2	22	9	0	0	0	0	0	1
1	1	1	3	3	110	296	40	2	0	5	8	5
1	2	1	3	1	27	4	0	0	2	0	0	4
1	2	1	3	2	32	24	2	2	0	1	1	3
1	2	1	3	3	87	75	23	2	0	0	7	3
1	2	1	1	1	66	9	42	0	1	0	0	0
1	2	1	1	2	38	27	36	2	1	0	0	0
1	2	1	1	3	87	57	36	1	0	0	0	0
1	2	1	4	1	9	1	26	3	1	0	0	0
1	2	1	4	2	41	8	11	1	0	1	0	0
1	2	1	4	3	42	28	5	0	0	0	0	0
1	3	1	4	1	12	1	1	0	0	0	0	0
1	3	1	4	2	18	12	3	2	0	1	0	0
1	3	1	4	3	35	26	3	6	0	2	0	0
1	3	1	1	1	19	7	38	1	0	0	0	0

Habitat ^b	Month	Year ^c	Site ^d	Level ^e	<u>L. hartmanni</u>	<u>L. trapidoi</u>	<u>L. yuilli</u>	<u>L. panamensis</u>	<u>L. tintinnabula</u>	<u>L. bifoliata</u>	<u>L. gomezi</u>	<u>W. rotundipennis</u>
1	3	1	1	2	17	3	22	0	0	0	0	0
1	3	1	1	3	66	20	54	0	0	1	0	0
1	3	1	3	1	23	3	15	2	0	0	1	4
1	3	1	3	2	40	2	6	0	0	0	1	4
1	3	1	3	3	92	112	32	2	0	4	6	8
h 1	4	1	4	1	13	2	90	2	32	0	0	1
1	4	1	4	2	16	4	51	2	1	0	0	0
1	4	1	4	3	12	11	14	0	0	1	0	0
1	4	1	1	1	61	19	35	0	3	0	0	0
1	4	1	1	2	20	11	10	0	1	0	0	0
1	4	1	1	3	59	78	21	0	0	0	0	0
1	4	1	3	1	40	0	2	0	1	0	0	5
1	4	1	3	2	66	10	2	0	0	0	1	1
1	4	1	3	3	295	197	90	7	0	6	22	5
1	5	1	4	1	30	8	2	8	8	0	0	0
1	5	1	4	2	26	16	5	0	0	0	0	0
1	5	1	4	3	20	15	0	1	0	0	0	0
1	5	1	1	1	85	12	2	0	9	0	0	0
1	5	1	1	2	18	13	1	0	0	0	0	0
1	5	1	1	3	49	35	4	0	0	0	0	0
1	5	1	3	1	55	3	1	1	0	1	0	1
1	5	1	3	2	71	3	0	0	0	0	0	2
1	5	1	3	3	153	58	66	12	0	8	11	1
1	6	1	4	1	38	0	1	2	0	0	0	0
1	6	1	4	2	38	7	2	6	0	0	0	0
1	6	1	4	3	19	10	0	4	0	1	0	0

Habitat ^b	Month	Year ^c	Site ^d	Level ^e	<u>L. hartmanni</u>	<u>L. trapidoi</u>	<u>L. yuilli</u>	<u>L. panamensis</u>	<u>L. tintinnabula</u>	<u>L. bifoliata</u>	<u>L. gomezi</u>	<u>W. rotundipennis</u>
1	6	1	1	1	265	8	15	8	4	0	0	0
1	6	1	1	2	94	16	25	2	0	0	0	0
1	6	1	1	3	155	16	24	32	0	1	0	0
1	6	1	3	1	7	0	0	0	0	0	0	0
1	6	1	3	2	1	0	0	0	0	0	0	0
1	6	1	3	3	3	6	2	4	0	2	4	0
1	7	1	4	1	94	15	5	2	0	2	0	0
1	7	1	4	2	58	25	1	4	0	9	0	1
1	7	1	4	3	20	23	4	8	0	4	0	0
1	7	1	1	1	59	3	1	0	0	0	0	0
g1	7	1	1	2	5	1	0	0	0	0	0	0
1	7	1	1	3	7	1	6	1	0	0	0	0
1	7	1	3	1	117	16	0	10	0	0	0	18
1	7	1	3	2	111	38	1	29	0	1	1	9
1	7	1	3	3	103	113	51	106	0	6	22	4
1	8	1	4	1	45	1	7	0	2	5	0	0
1	8	1	4	2	50	25	1	5	0	1	0	1
1	8	1	4	3	12	9	1	6	0	3	0	0
1	8	1	3	1	10	0	0	1	0	1	0	0
1	8	1	3	2	9	5	1	0	0	2	0	1
1	8	1	3	3	39	11	7	1	0	15	1	1
1	8	1	1	1	16	0	1	0	0	0	0	0
1	8	1	1	2	30	2	5	0	0	0	0	0
1	8	1	1	3	57	17	6	1	0	0	0	0
2	3	1	A	1	20	0	1	1	0	0	3	4
2	3	1	B	1	24	0	0	3	0	0	7	16

Habitat ^b	Month	Year ^c	Site ^d	Level ^e	<u>L. hartmanni</u>	<u>L. trapidoi</u>	<u>L. yuilli</u>	<u>L. panamensis</u>	<u>L. tintinnabula</u>	<u>L. bifoliata</u>	<u>L. gomezi</u>	<u>W. rotundipennis</u>
2	3	1	D	1	65	2	4	8	1	0	2	27
2	3	1	C	1	37	0	12	2	0	0	39	10
2	3	1	E	1	145	19	96	9	0	2	75	3
2	3	1	F	1	126	15	36	5	0	1	50	31
2	4	1	A	1	23	1	1	0	0	0	2	0
f 2	4	1	B	1	17	0	0	0	0	0	2	1
2	4	1	D	1	35	3	10	0	0	0	0	19
2	4	1	C	1	19	1	0	2	0	0	13	6
2	4	1	E	1	71	2	4	0	0	0	33	10
g 2	4	1	F	1	9	0	1	2	0	5	11	3
2	5	1	A	1	8	0	0	1	0	0	2	2
2	5	1	B	1	41	1	0	1	0	0	10	7
2	5	1	D	1	99	2	10	0	0	0	16	15
2	5	1	C	1	11	0	0	3	0	0	12	1
2	5	1	E	1	61	3	7	8	0	0	28	1
2	5	1	F	1	25	1	0	0	0	2	5	2
2	6	1	A	1	13	2	0	0	0	0	0	0
2	6	1	B	1	15	0	0	1	0	0	1	1
2	6	1	D	1	72	3	1	54	0	0	1	0
2	6	1	C	1	2	0	0	0	0	0	1	4
2	6	1	E	1	43	2	11	4	0	0	5	2
2	6	1	F	1	10	0	1	7	0	0	4	2
2	7	1	A	1	10	0	0	0	0	0	0	2
2	7	1	B	1	84	1	0	1	1	0	14	3
2	7	1	D	1	65	9	18	11	0	0	3	2
2	7	1	C	1	3	0	0	0	0	0	7	2

Habitat ^b	Month	Year ^c	Site ^d	Level ^e	<u>L. hartmanni</u>	<u>L. trapidoi</u>	<u>L. yuilli</u>	<u>L. panamensis</u>	<u>L. tintinnabula</u>	<u>L. bifoliata</u>	<u>L. gomezi</u>	<u>W. rotundipennis</u>
2	7	1	E	1	86	8	2	6	0	0	3	2
2	7	1	F	1	29	0	7	0	0	0	10	5
2	8	1	A	1	1	0	0	0	0	0	0	0
2	8	1	B	1	5	0	0	0	0	1	1	0
2	8	1	D	1	13	0	0	1	0	0	0	0
2	8	1	C	1	10	0	1	0	0	0	8	10
2	8	1	E	1	33	2	3	3	0	0	10	9
2	8	1	F	1	31	0	1	0	0	0	6	17

^aThe number under each species for each catch represents the actual number of individuals taken.

^b1 = forest, 2 = clearing.

^c0 = 1970, 1 = 1971.

^d1 = Buenos Aires 1 forest site, 2 = Providencia forest site, 3 = Tiroteos forest site, and letters A-F represent the clearing sites.

^e1 = ground, 2 = understory, 3 = canopy.

^fEnd points for 1st (X) axis of the ordination of the catches in species space.

^gEnd points for 2nd (Y) axis of the ordination of the catches in species space.

^hEnd points for 3rd (Z) axis of the ordination of the catches in species space.

Table II-42. Summary of the Vertical Stratification of Man-biting Activity Within the Forest by C. pseudodiabolicus, C. gabaldoni, and All Species Combined.

Species and Elevation	No. Taken	$M_G \times 100$	% M_G
<u>C. pseudodiabolicus</u>			
Ground	2592	59	20.6
Understory	5017	114	39.7
Canopy	7261	114	39.7
<u>C. gabaldoni</u>			
Ground	61	6	8.1
Understory	269	20	27.0
Canopy	896	48	64.9
All Species			
Ground	2692	63	16.4
Understory	5531	136	35.3
Canopy	8981	186	48.3

CERATOPOGONIDAE

RESULTS

A total of 21,188 specimens of Culicoides were taken in the man-biting catches. Culicoides pseudodiabolicus strongly dominated this biting activity at both the forest and clearing habitats, accounting for 18,242 or 86.1% of the specimens taken. Biting activity was primarily nocturnal (Fig II-27, Tables II-37, II-38; however, the second most abundant forest species, C. gabaldoni was diurnal Fig. II-28). There appears to be greater species diversity during the day catches and work is still continuing on some of the less abundant species.

The domination of C. pseudodiabolicus is such that the pattern of biting activity for all species combined is very similar to that of this species (Figs. II-27, II-29). Within the forest the biting activity of this species increased rapidly after sunset but became somewhat reduced during the succeeding two catch periods. Biting increased during catch period 21 and a high level of activity was maintained until 0500 hours. A decline in biting activity then began during catch period 05 and lasted to 1000 hours. The pattern of a rapid increase in biting activity after sunset in catch period 18 followed by a moderate reduction in the succeeding two periods was observed at all three forest sites and at all three levels (Tables II-39, II-40). The relatively low diurnal level of biting activity maintained by C. pseudodiabolicus appeared to be concentrated in the understory (Table II-40). In the clearing biting activity by this species appeared to begin with sunset and rapidly attained a high level of intensity during the first catch period after sunset. This activity continued to gradually increase

until 0100 hours and then began a rather slow decline (Table II-41).

The vertical stratification of biting activity presented in Table II-42 indicates that C. pseudodiabolicus has some arboreal preference. The pattern of vertical stratification was quite similar at each of the three forest sites (Table II-43). In contrast to the apparent concentration of biting activity in the understory during the day, this species nocturnal biting activity was greatest in the canopy. In the clearing, C. pseudodiabolicus was most abundant at the two sites adjacent to the forest and was least numerous at those sites most closely associated with cultivation, i.e., B and F (Table II-44). However, it was remarkably abundant at the exposed site near the center of the clearing. The seasonal distribution of biting activity suggests that the population level of this species becomes greatly reduced during the dry season, although a small adult population persists, at least in those years with an abnormally mild dry season (Table II-45). The adult population appears to increase gradually with the beginning of the rainy season and attains a maximum level from August through December.

The second most abundant forest species, C. gabaldoni, accounted for only 7.1% of the specimens taken in the forest catches. This diurnal species attained a maximum level of biting activity between 1200 and 1600 hours (Fig II-28 and Table II-37). C. gabaldoni is arboreal but the percentage of its biting activity occurring at ground level was considerably greater at the two Buenos Aires sites than at the other forest sites (Table II-43). This species was distinctly more abundant at the Tiroteos site. Adults of this species are present throughout the year, but the population level becomes somewhat reduced toward the end of the dry season. The apparent decline during August and September (Table II-45) can be attributed to the fact that no collections were made at the Tiroteos site

during those months.

The remaining biting activity within the forest was divided among a large number of infrequently occurring species, some of which appear to be undescribed (Table II-46). The identification of some of these species has proven to be quite difficult and work toward this end continues. The more abundant of these species include the diurnal C. spurius, paraensis, fieldi and leoni, the apparently crepuscular mirsa, and the nocturnal lanei, galindoi and uniradialis.

Unfortunately the Culicoides taken in the diurnal clearing collections were seldom preserved, but records of their occurrence were maintained so that a temporal pattern for all species combined could be developed (Table II-38). Diurnal activity in the clearing is almost negligible but at night it became comparable to that within the forest. Relatively small numbers of C. fusipalpis and C. ignacioi, two species closely related to C. pseudodiabolicus, were also taken in the nocturnal clearing catches. The temporal pattern of their biting activity is presented in Table II-41. Both of these species show a decline in activity after 0100 hours. C. fusipalpis was most abundant at clearing site B which is located in an area of cultivation and is the site where C. pseudodiabolicus was least numerous.

Table II-37. Temporal Patterns of Man-biting Activity Within the Forest by C.pseudodiabolicus, C. gabaldoni, and All Species Combined.

Catch period	<u>C. pseudodiabolicus</u>		<u>C. gabaldoni</u>		<u>All Species</u>	
	No. Taken	$M_G \times 10$	No. Taken	$M_G \times 10$	No. Taken	$M_G \times 10$
06-07	---	--	—	—	---	--
07-08	479	11	4	2	551	13
08-09	379	9	30	10	538	12
09-10	274	5	40	13	417	8
10-11	111	3	88	17	296	5
11-12	86	2	173	28	308	6
12-13	69	2	258	45	366	7
13-14	41	1	161	30	263	4
14-15	71	2	147	40	316	7
15-16	136	3	163	40	406	8
16-17	72	2	94	29	215	6
17-18	59	3	67	25	261	8
18-19	787	24	1	1	810	21
19-20	688	15	0	0	697	14
20-21	633	15	0	0	642	14
21-22	756	24	0	0	763	22
22-23	1409	29	0	0	1419	26
23-24	1300	25	0	0	1320	23
24-01	1722	37	0	0	1749	36
01-02	931	23	0	0	934	23
02-03	1284	31	0	0	1295	30
03-04	1206	32	0	0	1223	32
04-05	1948	37	0	0	1979	37
05-06	429	19	0	0	436	19
TOTAL	14,870		1226		17,204	

Table II-38 Temporal Pattern of Man-biting Activity Within the Clearing
by All Species Combined.

<u>Catch Period</u>	<u>No. Taken</u>	<u>M_Gx 10</u>
06-07	---	--
07-08	33	1
08-09	43	1
09-10	35	1
10-11	35	1
11-12	31	1
12-13	32	1
13-14	48	1
14-15	21	1
15-16	17	0
16-17	7	0
17-18	2	0
18-19	157	23
19-20	314	32
20-21	370	32
21-22	258	32
22-23	542	38
23-24	404	33
24-01	405	41
01-02	371	28
02-03	250	24
03-04	192	16
04-05	224	22
05-06	193	20
TOTAL	3984	

Table II- 39 Temporal Patterns of Man-biting Activity by C. pseudodiabolicus for Three Forest Sites.

Catch Period	Buenos Aires I		Providencia		Tiroteos	
	No. Taken	$M_G \times 10$	No. Taken	$M_G \times 10$	No. Taken	$M_G \times 10$
06-07	---	--	---	--	---	--
07-08	134	24	125	11	90	8
08-09	131	21	120	9	72	6
09-10	133	16	42	4	17	2
10-11	46	7	19	2	5	1
11-12	27	4	18	2	4	1
12-13	19	4	27	3	3	1
13-14	12	2	18	2	2	0
14-15	15	2	29	3	11	1
15-16	32	5	33	3	5	1
16-17	27	4	15	2	14	2
17-18	40	6	8	1	11	2
18-19	436	39	133	12	218	21
19-20	470	27	88	6	130	11
20-21	415	22	139	11	79	9
21-22	528	44	134	13	94	16
22-23	763	40	332	23	314	22
23-24	414	21	680	40	206	18
24-01	619	40	701	39	402	33
01-02	457	31	336	14	138	26
02-03	365	21	514	33	405	38
03-04	250	12	451	26	505	62
04-05	126	20	308	17	1514	102
05-06	24	7	119	13	286	45

Table II-4. Temporal Patterns of Man-biting Activity by C. pseudodiabolicus at Three Levels in the Forest.

Catch Period	Ground		Understory		Canopy	
	No. Taken	$M_G \times 10$	No. Taken	$M_G \times 10$	No. Taken	$M_G \times 10$
06-07	---	--	---	--	---	--
07-08	214	15	210	15	55	5
08-09	135	10	177	12	67	6
09-10	62	5	160	9	52	3
10-11	22	2	70	6	19	1
11-12	18	2	45	4	23	1
12-13	15	2	34	3	20	2
13-14	15	2	19	2	7	1
14-15	16	2	36	3	19	1
15-16	11	1	65	5	60	3
16-17	8	1	40	4	24	2
17-18	15	3	30	5	14	3
18-19	120	13	257	25	410	37
19-20	89	6	199	17	400	26
20-21	47	5	244	17	342	27
21-22	54	7	246	26	456	35
22-23	251	12	564	42	594	42
23-24	279	16	416	30	605	32
24-01	178	15	380	33	1164	88
01-02	119	9	269	19	543	52
02-03	157	12	258	25	869	79
03-04	200	17	571	35	435	50
04-05	465	18	574	37	909	68
05-06	102	13	153	19	174	25

Table II-41. Temporal Patterns of Nocturnal Man-biting Activity Within the Clearing by

C. pseudodiabolicus, C. fusipalpis and C. ignacioi.

Catch Period	<u>C. pseudodiabolicus</u>		<u>C. fusipalpis</u>		<u>C. ignacioi</u>	
	No. Taken	$M_G \times 10$	No. Taken	$M_G \times 10$	No. Taken	Arith. Mean
17-18	1	0	0	0	0	0.00
18-19	140	19	11	17	3	0.08
19-20	270	24	18	35	20	0.56
20-21	322	25	32	39	14	0.39
21-22	232	26	17	24	7	0.19
22-23	496	28	31	43	14	0.39
23-24	375	29	16	23	10	0.28
24-01	365	34	20	27	16	0.44
01-02	358	25	9	18	1	0.03
02-03	243	22	2	4	2	0.06
03-04	181	14	8	14	2	0.06
04-05	211	20	9	17	3	0.08
05-06	<u>178</u>	16	<u>7</u>	13	<u>1</u>	0.03
TOTAL	3372		180		93	

Table II-43. Summary of the Vertical Stratification of Man-biting Activity of C. pseudodiabolicus and C. gabaldoni.

Site and Elevation	<u>C. pseudodiabolicus</u>			<u>C. gabaldoni</u>		
	No. Taken	$M_G \times 10$	% M_G	No. Taken	$M_G \times 100$	% M_G
Buenos Aires I						
Ground	929	11	23.9	34	14	29.2
Understory	1910	18	39.1	58	16	33.3
Canopy	2644	17	37.0	42	18	37.5
Providencia						
Ground	593	4	14.8	5	2	4.3
Understory	1454	11	40.7	34	13	28.3
Canopy	2342	12	44.4	101	31	67.4
Tiroteos						
Ground	1009	6	21.4	6	2	1.0
Understory	1423	11	39.3	154	41	20.4
Canopy	2093	11	39.3	723	158	78.6
Buenos Aires II						
Ground				16	7	22.6
Understory				23	11	35.5
Canopy				30	13	41.9

Table II-44. Summary of Man-biting Activity at the Six Clearing Sites for C. pseudodiabolicus, C. fusiipalpis,
C. ignacioli, and All Species Combined.

Site	<u>C. pseudodiabolicus</u>			<u>C. fusiipalpis</u>			<u>C. ignacioli</u>			All Species		
	No. Taken	M _G x 10	% M _G	No. Taken	M _G x 100	% M _G	No. Taken	Arith. mean	%	No. Taken	M _G x 10	% M _G
A	287	12	8.5	26	20	15.4	6	0.08	6.5	379	26	9.5
B	126	8	5.6	71	48	36.9	10	0.13	10.8	227	16	5.9
C	793	30	21.1	13	11	8.5	8	0.10	8.6	852	45	16.5
D	932	34	23.9	11	8	6.2	6	0.08	6.5	1041	69	25.3
E	1034	49	34.5	47	32	24.6	60	0.78	64.5	1234	100	36.6
F	200	9	6.3	12	11	8.5	3	0.04	3.2	251	17	6.2

Table II-45 Man-biting Activity by Month Within the Forest by C. pseudodiabolicus, C. gabaldoni and All Species Combined.

Month	<u>C. pseudodiabolicus</u>			<u>C. gabaldoni</u>			All Species	
	No. taken	M _G x 10	No. Taken	M _G x 100	No. Taken	M _G x 10	No. Taken	M _G x 10
January	1176	10	34	16	1237	12		
February	49	1	49	16	137	2		
March	93	1	27	9	157	3		
April	429	3	24	10	499	5		
May	1343	6	96	19	1522	8		
June	1081	7	295	55	1596	12		
July	1658	8	325	47	2433	12		
August	2812	27	44	16	2906	27		
September	1166	19	13	6	1193	20		
October	1068	17	53	26	1167	20		
November	1418	29	145	23	1613	35		
December	2577	23	121	37	2744	32		

Table II-46 Systematic Arrangement of the Culicoides of the Providencia Study Area.

Subgenus *Hoffmania* Fox

venustus group

- filariferus* Hoffman, 1939
- foxi* Ortiz, 1951
- fusipalpis*, Wirth and Blanton, 1973
- ignacioi* Forattini, 1957
- insignis* Lutz, 1931
- pseudodiabolicus* Fox, 1946

hylas group

- heliconiae* Fox and Hoffman, 1944
- hylas* Macfie, 1940
- palpalis* Macfie, 1948
- polypori* Wirth and Blanton, 1968
- verecundus* Macfie, 1948

Subgenus *Avaritia* Fox

- pusillus* Lutz, 1913

Subgenus *Anilomyia* Vargas

covagarciai group

- metagonatus* Wirth and Blanton, 1956
- sp. F
- covagarciai* Ortiz, 1950

Subgenus *Drymadesmyia* Vargas

daedalus group

- antefurcatus* Wirth and Blanton, 1959

Subgenus Oecaeta

limai group

vernoni Wirth and Blanton, 1973

monticola Wirth and Lee, 1967

limai Barretto, 1944

acotylus group

lanei Ortiz, 1950

*venezuelensis Ortiz and Mirsa, 1950

reticulatus group

dicrourous Wirth and Blanton, 1955

paucien fuscatus Barbosa, 1947

macrostigma Wirth and Blanton, 1953

fluvialis group

balsapambensis Ortiz and Leon, 1955

castillae Fox, 1946

fluvialis Macfie, 1950

leopoldoi Ortiz, 1952

propiipennis Macfie, 1948

tetrathyris Wirth and Blanton, 1959

albuquerquei, Wirth and Blanton, 1973

transferrans group

eublepharus Macfie, 1948

patulipalpis Wirth and Blanton, 1959

rangeli Ortiz and Mirsa, 1952

leoni group

close to fieldi Wirth and Blanton, 1956

glabellus Wirth and Blanton, 1956

leoni Barbosa, 1952

close to benarrochei Ortiz and Mirsa, 1952

sp. C

sp. I

debilipalpis group

close to debilipalpis Lutz, 1913

gabaldoni Ortiz, 1954

ginesi Ortiz, 1952

guerrai Wirth and Blanton, 1971

mirsaе Ortiz, 1953

spurius Wirth and Blanton, 1959

close to paraensis (Goeldi), 1905

close to glabrior Macfie, 1940

sp. B

sp. L

sp. N

pachymerus group

obnoxius Fox, 1952

uniradialis Wirth and Blanton, 1953

almirantei Wirth and Blanton, 1959

Ungrouped species

sp. A

sp. G

sp. H

sp. O

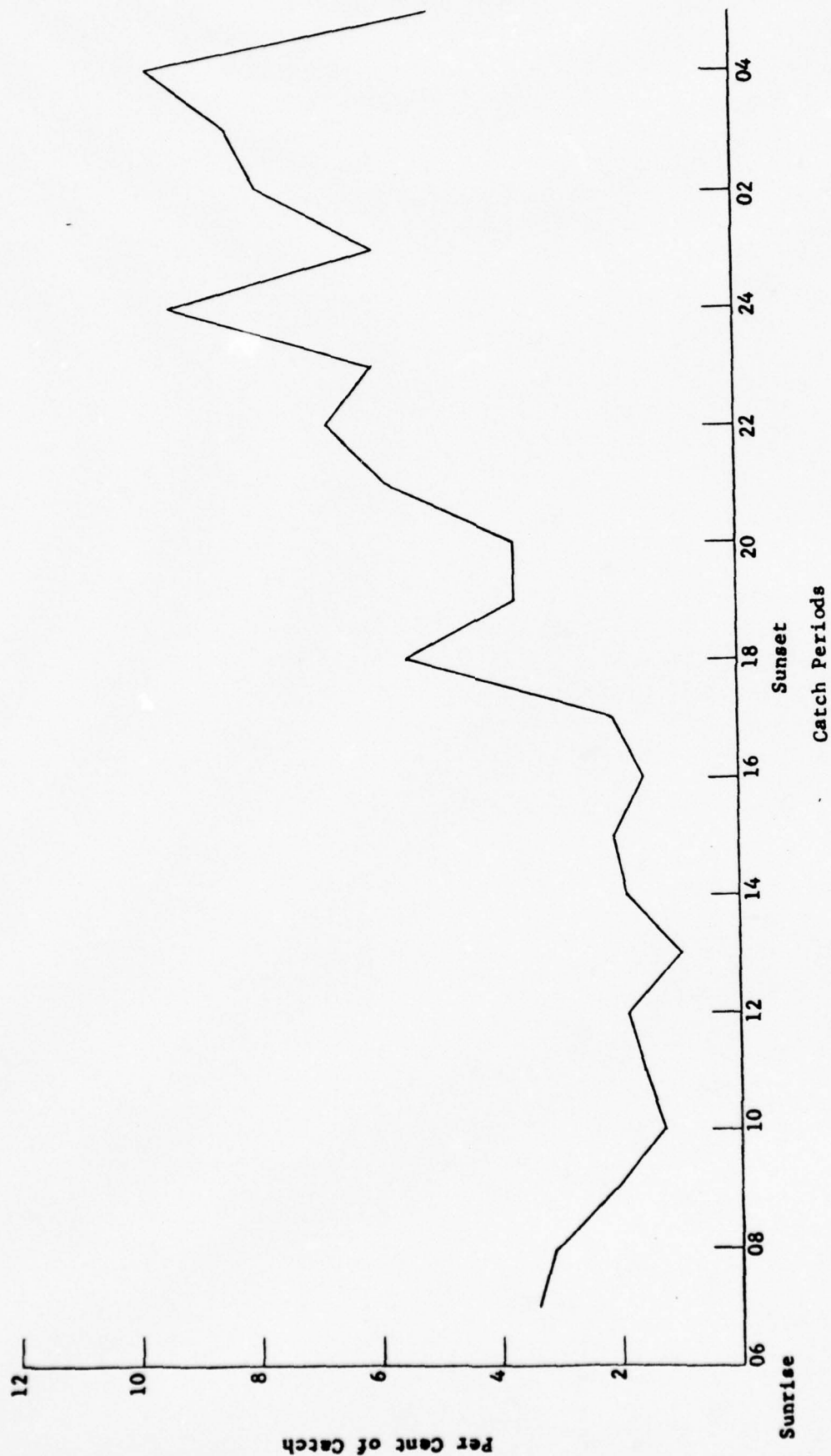


Figure II-27 Temporal pattern of man-biting activity by all species of Culicoides combined. This pattern is based on geometric means converted to percentages. Each catch period approximates the corresponding hour.

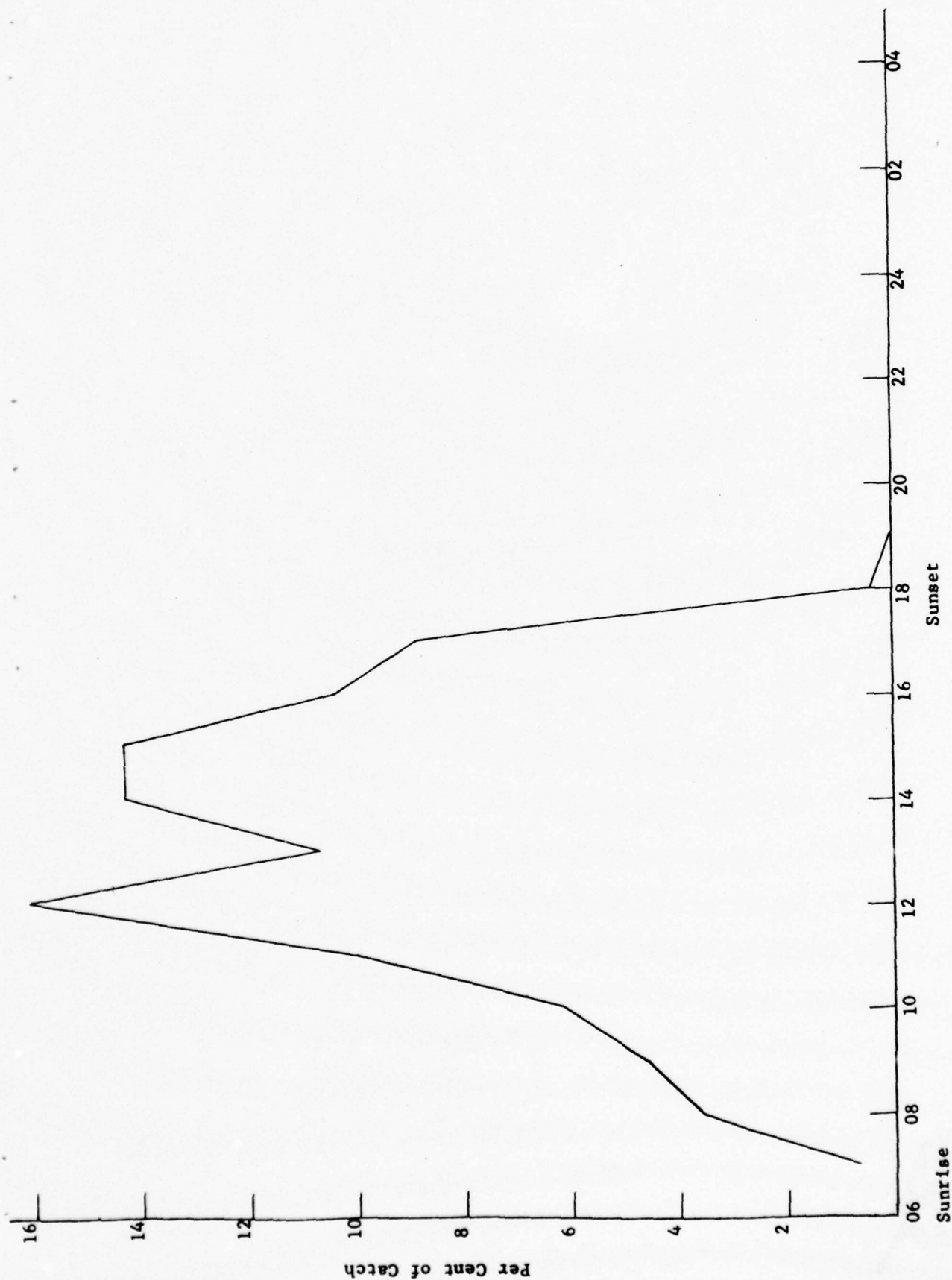


Figure II-28. Temporal pattern of man-biting activity in forest by *C. gabaldoni* based on geometric means converted to percentages. Each catch period approximates the corresponding hour.

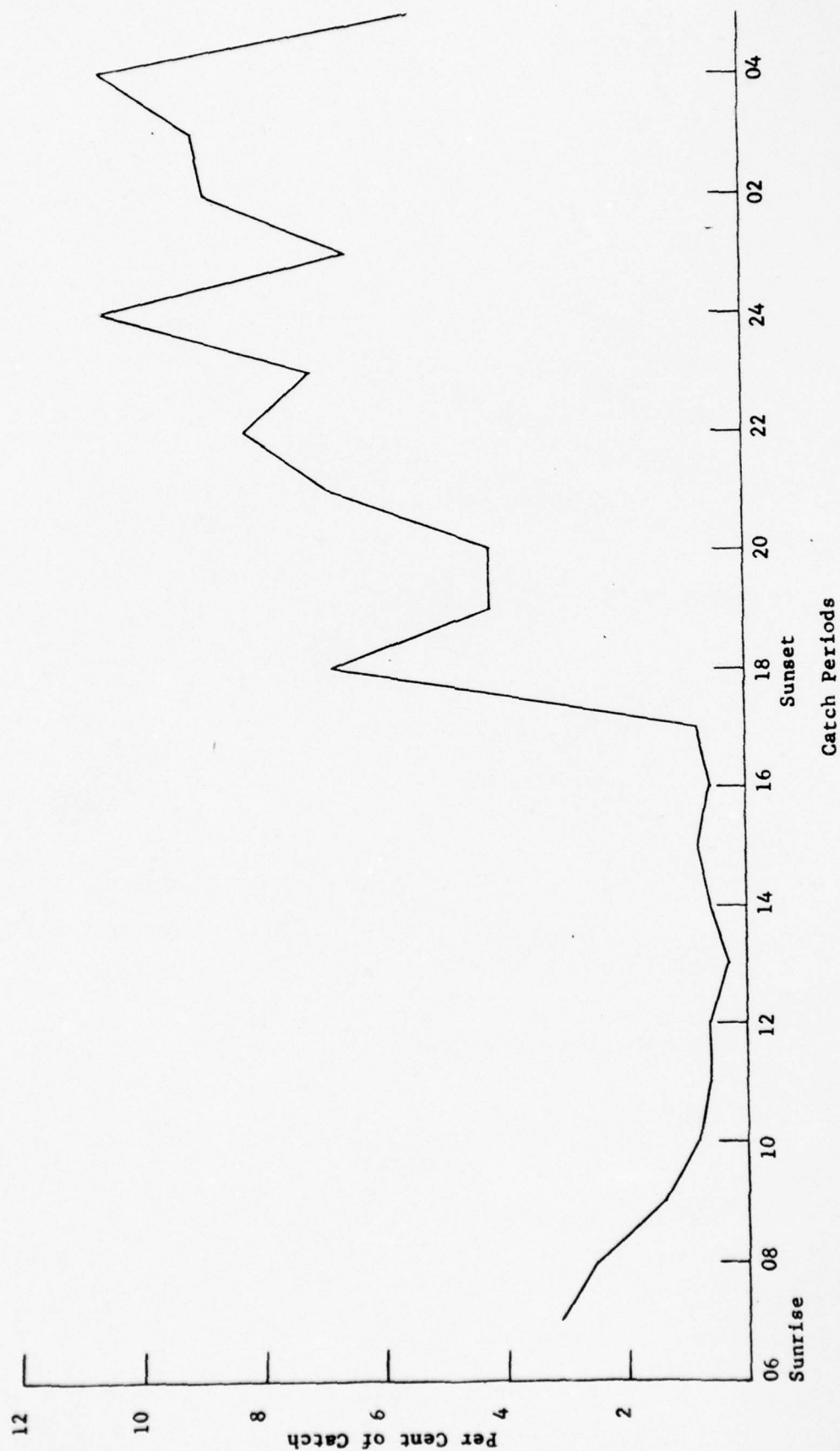


Figure II-29. Temporal pattern of man-biting activity in forest by C. pseudodiaboli based on geometric means converted to percentages. Each catch period approximates the corresponding hour.

TABANIDAE

RESULTS

A check list of the Tabanidae of the Providencia region is presented in Table II-47. Tabulation of the raw data has been completed and is now being transferred to computer cards for final analysis. The following discussion is a preliminary summary of portions of the field data. After our analyses have been completed, a detailed report will be presented as a supplement.

The vertical distribution of Dichelacera chocoensis (Tables II-48, II-49) shows that this tabanid has a very pronounced preference for the ground level and is only occasionally found in the canopy. This distinct preference for the ground level occurs at all of the sites but is especially striking at the Tiroteos, the site of this species' greatest abundance (Tables II-49, II-50). The biting activity of this species reached a maximum in the afternoon from approximately 1400 to 1800 hours. Catch period 17 was the first period of the night platform studies, and thus the peak of biting activity observed for this period may have partially been due to an increase in the numbers of this species in the vicinity of the platform site resulting from their attraction to the workers as they passed through a portion of

Table II-47

Checklist of Tabanidae of the Providencia region

- Esenbeckia (Esenbeckia) translucens (Macquart) 1846
- Fidena (Fidena) eriomeroides (Lutz) 1909
- Fidena (Fidena) flavipennis Kröber 1931
- Fidena (Fidena) schildi (Hine) 1925
- Chrysops leucospilus Wiedmann 1828
- Chrysops mexicanus Kröber 1925
- Chrysops nexosus Fairchild (not yet described)
- Chrysops soror Kröber 1925
- Chrysops varians var. tardus Wiedmann 1828
- Stenotabanus (Stenotabanus) incipiens (Walker) 1860
- Stenotabanus (Stenotabanus) obscurus Kröber 1929
- Stenotabanus (Stenotabanus) sordidatus Fairchild 1958
- Himantostylus intermedius Lutz 1913
- Diachlorus curvipes (Fabricius) 1805
- Bolbodimyia erythrocephala (Bigot) 1892
- Bolbodimyia galindoi Fairchild 1964
- Bolbodimyia philipi Stone 1954
- Selasoma tibiale (Fabricius) 1805
- Chlorotabanus inanis (Fabricius) 1787
- Chlorotabanus mexicanus (Linnaeus) 1758
- Phaeotabanus phaeopterus Fairchild 1964
- Dichelacera (Dichelacera) chocoensis Fairchild and Philip 1960
- Dichelacera (Dichelacera) regina Fairchild 1940
- Dichelacera (Dichelacera) scapularis Macquart 1847
- Dichelacera (Dichelacera) submarginata Lutz 1915
- Dichelacera (Dichelacera) marginata Macquart 1847

Table II- 47 (cont)

- Dichelacera* (*Desmatochelacera*) *trasposita* Walker 1854
- Dichelacera* (*Idiochelacera*) *subcallosa* Fairchild and Philip 1960
- Catachlorops* (*Amphichorops*) *flavissimus* (to be described)
- Catachlorops* (*Psalidia*) *fulmineus* (Hine) 1920
- Catachlorops* (*Psalidia*) *fulmineus* (Hine) 1920 var. *ocellatus* Enderlein 1925
- Catachlorops* (*Psalidia*) *umbratus* (Hine) 1920
- Catachlorops* (*Psarochlorops*) *quadrimaculatus* (Macquart) 1846
- Stibasoma* (*Stibasoma*) *flaviventre* (Macquart) 1848
- Stibasoma* (*Stibasoma*) *fulvohirtum* (Wiedemann) 1828
- Stibasoma* (*Stibasoma*) *panamensis* Curran 1934
- Philipotabanus* (*Philipotabanus*) *magnificus* (Kröber) 1934
- Philipotabanus* (*Philipotabanus*) *nigrinubilus* (Fairchild) 1953
- Philipotabanus* (*Melasmatabanus*) *fascipennis* (Macquart) 1846
- Philipotabanus* (*Melasmatabanus*) *criton* (Kröber) 1934
- Philipotabanus* (*Mimotabanus*) *fucosus* Fairchild 1958
- Philipotabanus* (*Mimotabanus*) *annectans* Fairchild 1975
- Philipotabanus* (*Mimotabanus*) *porteri* Fairchild 1975
- Stypommisa* *captiroptera* (Kröber) 1930
- Stypommisa* *jaculatrix* (Fairchild) 1942
- Stypommisa* *modica* (Hine) 1920
- Stypommisa* *maruccii* (Fairchild) 1947
- Stypommisa* *pequeniensis* (Fairchild) 1942
- Stypommisa* *serena* (Kröber) 1931
- Stypommisa* sp. N
- Leucotabanus* *exaestuans* (Linnaeus) 1758
- Leucotabanus* *flavinotum* (Kröber) 1934

Table II-47 (cont)

Poeciloderas quadripunctatus (Fabricius) 1805 var. *amabilinus* Philip 1960

Tabanus antarcticus Linnaeus 1758

Tabanus dorsiger Wiedemann 1821 var. *dorsovittatus* Macquart 1855

Tabanus dorsiger ssp. *modestus* Wiedemann 1828

Tabanus dorsiger ssp. *stenocephalus* Hine 1906

Tabanus macquarti Schiner 1868

Tabanus thiemana ssp. *surifer* Fairchild 1964

Tabanus pungens Wiedemann 1828

Table II-48 Dichelacera choocoensis diurnal temporal and vertical patterns of biting activity.

Period beginning*	07	08	09	10	11	12	13	14	15	16	17	18	Totals (%)
No. Periods	51	56	58	58	58	57	57	57	57	51	34	33	
Ground Level													
No. Taken	38	24	55	140	108	130	264	456	421	304	361	2	2303
No./Period	0.74	0.43	0.95	2.41	1.86	2.28	4.63	8.00	7.38	5.96	10.62	0.06	3.67 (86)
Understory Level													
No. Taken	23	16	12	18	0	6	19	26	54	32	86	8	300
No./Period	0.45	0.28	0.21	0.31	0	0.11	0.33	0.46	0.95	1.59	2.53	0.24	0.48 (11)
Canopy Level													
No. Taken	20	3	0	3	1	3	3	3	14	18	20	0	88
No./Period	0.39	0.05	0	0.05	0.02	0.05	0.05	0.05	0.24	0.35	0.59	0	0.14 (3)
Total													
No. Taken	81	43	67	161	109	139	286	485	489	354	467	10	
No./Period	0.53	0.26	0.38	0.92	0.63	0.81	1.67	2.84	2.86	2.31	4.58	0.10	

* The time between sunrise and sunset divided into 12 equal periods; the hour designations approximate the beginning of each period which varies with day length throughout the year. Periods with heavy rain which prevented collecting are excluded. The first day period is excluded and the first night period is included.

Table II-49 Vertical distribution of Dichelacera chocoensis
at four forest collecting sites.

	No. Taken	No./Period	%
Buenos Aires I			
Ground level	190	1.28	70
Understory	61	0.41	23
Canopy	18	0.12	7
Buenos Aires II			
Ground level	71	0.52	69
Understory	28	0.20	27
Canopy	4	0.03	4
Providencia			
Ground level	780	4.48	82
Understory	130	0.75	14
Canopy	35	0.20	4
Tiroteos			
Ground level	1262	7.56	92
Understory	81	0.43	6
Canopy	31	0.18	2

Table II-50. Temporal distribution of Dichelacera chocoensis biting activity at different forest sites.

Period beginning	07	08	09	10	11	12	13	14	15	16	17	18	Total
Buenos Aires I													
No. Taken	12	2	7	11	4	9	27	25	41	43	79	9	269
No. Periods	24	36	39	39	39	36	39	39	39	36	39	42	447
No./Period	0.50	0.56	0.18	0.28	0.10	0.25	0.69	0.64	1.05	1.19	2.02	0.21	0.60
Buenos Aires II													
No. Taken	11	1	6	7	1	4	3	8	32	30			103
No. Periods	39	39	42	42	42	42	14	42	42	39			411
No./Period	0.28	0.03	0.14	0.17	0.02	0.10	0.21	0.19	0.76	0.77			0.25
Providencia													
No. Taken	31	23	21	50	61	68	95	145	165	109	177	0	945
No. Periods	45	48	48	48	48	48	45	45	45	39	33	30	522
No./Period	0.69	0.48	0.44	1.04	1.27	1.42	2.11	3.22	3.67	2.79	5.36	0	1.81
Tiroteos													
No. Taken	27	17	33	93	43	58	161	307	251	172	211	1	1374
No. Periods	45	45	45	45	45	45	45	45	45	39	30	27	501
No./Period	0.60	0.38	0.73	2.07	0.96	1.29	3.58	6.82	5.58	4.41	7.03	0.04	2.74

the forest to reach the platform site. The slight decline in activity during catch period 16 at ground level coincided with a slight increase in the understory level. A small decrease in the biting activity occurred during catch period 16 at the Providencia and Tiroteos sites but did not occur at the Buenos Aires sites. D. chocoensis had a distinct pattern of seasonal abundance (Table II-51). Adults were not present from January through March and very few were found in December and April. A well defined peak of the adult population occurred in June and July, at which time it was very abundant in the forested areas of the Providencia region.

Stypommisa modica had a pronounced preference for the canopy at all four platform sites and was most abundant at the Providencia and Tiroteos sites (Tables II-52, II-53). A peak in biting activity occurred from approximately 1100 to 1200 hours, which was followed by a gradually decreasing level of activity throughout the remainder of the diurnal periods (Tables II-52, II-54). However, at the Buenos Aires II site a peak in biting activity did not occur until catch period 13, and in the understory there was a rather uniform period of biting activity extending to about 1600 hours. The adult population of Stypommisa modica was quite seasonal (Table II-55). A distinct peak in abundance occurred during April and was followed by a decline that appeared to be rapid at first and then quite slow. By November all of the adults had disappeared and none were encountered again until February.

Additional information about the diurnal biting activity and seasonal distribution of various species of Tabanidae was acquired by collecting from two horses or mules all individuals of this family over a standardized period of time at the edge of forested areas. The first collections were

Table II-51 Seasonal distribution of Dichelacera chocoensis biting activity.

	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
No. Taken	0	0	0	6	221	1082	1032	114	85	138	12	1
No. Periods	138	168	165	165	210	192	204	120	129	129	126	135
No./Period	0	0	0	0.04	1.05	5.64	5.06	0.95	0.66	1.07	0.10	0.01

Table II-52. Styponmisa modica diurnal temporal and vertical patterns of biting activity.

Period beginning*	07	08	09	10	11	12	13	14	15	16	17	sunset 18	Totals ⁺ (%)
No. Periods	52	56	58	58	58	57	57	57	57	50	34	33	
Ground Level													
No. Taken	0	0	0	1	5	7	10	7	4	1	0	0	35
No./Period	0	0	0	0.02	0.09	0.12	0.18	0.12	0.07	0.02	0	0	0.06 (4)
Understory Level													
No. Taken	0	0	0	10	23	20	20	23	28	15	0	0	143
No./Period	0	0	0.07	0.17	0.40	0.37	0.37	0.40	0.49	0.30	0	0	0.24 (19)
Canopy Level													
No. Taken	1	11	32	90	121	98	73	65	58	37	3	0	589
No./Period	0.02	0.20	0.55	1.55	2.09	1.72	1.28	1.14	1.02	0.74	0.09	0	0.99 (77)
Total													
No. Taken	1	11	36	101	149	125	103	95	90	53	3	0	
No./Period	0.01	0.06	0.21	0.58	0.86	0.73	0.60	0.56	0.53	0.35	0.03	0	

* The time between sunrise and sunset divided into 12 equal periods; the hour designations approximate the beginning of each period which varies with day length throughout the year. Periods with heavy rain which prevented collecting are excluded. The first day period is excluded and the first night period is included.

+ Catch period 18 excluded

Table II-53. Vertical distribution of Stypommisa modica
at four forest collecting sites.

	No. Taken	No./Period	%
Buenos Aires I			
Ground level	12	0.09	15
Undersotry	8	0.06	10
Canopy	60	0.44	75
Buenos Aires II			
Ground level	7	0.05	8
Understory	26	0.19	28
Canopy	58	0.43	64
Providencia			
Ground level	12	0.07	4
Understory	53	0.32	15
Canopy	282	1.72	81
Tiroteos			
Ground level	4	0.02	2
Understory	56	0.35	22
Canopy	189	1.20	76

Table II-54. Temporal distribution of Stypommisa modica biting activity at different sites.

Period beginning	07	08	09	10	11	12	13	14	15	16	17	Totals
Buenos Aires I												
No. Taken	0	0	1	3	21	12	17	11	11	4	0	80
No. Periods	27	36	39	39	39	36	39	39	39	36	39	408
No./Period	0	0	0.03	0.08	0.54	0.33	0.44	0.28	0.28	0.11	0	0.20
Buenos Aires II												
No. Taken	0	2	8	9	8	12	22	15	9	6	91	91
No. Periods	39	39	42	42	42	42	42	42	42	36	36	408
No./Period	0	0.05	0.19	0.21	0.19	0.29	0.52	0.36	0.21	0.17	0.03	0.22
Providencia												
No. Taken	0	5	17	65	64	56	35	32	44	28	1	347
No. Periods	45	48	48	48	48	48	45	45	45	39	33	492
No./Period	0	0.10	0.35	1.35	1.33	1.17	0.78	0.71	0.98	0.72	0.03	0.70
Tiroteos												
No. Taken	1	4	10	24	56	45	29	37	26	15	2	249
No. Periods	45	45	45	45	45	45	45	45	45	39	30	474
No./Period	0.02	0.09	0.22	0.53	1.24	1.00	0.64	0.82	0.58	0.38	0.07	0.52

Table II-55 Seasonal distribution of Stypomys modica biting activity.

	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
No. Taken	0	33	107	243	131	115	78	29	22	9	0	0
No. Periods*	129	159	156	156	204	177	189	114	126	123	120	129
No./Period	0	0.21	0.68	1.56	0.64	0.65	0.41	0.25	0.17	0.07	0	0

* Catch period 18 excluded

about 3-5 hours in duration, but they were soon extended to cover 11 catch periods, which corresponded with the interval of time from approximately 0700 to 1800 hours. The tabanids were collected individually in 5-dram vials, and at the end of each catch period, the accumulated vials were placed in an appropriately labeled plastic bag. The specimens were then processed in a manner similar to that already described for the insects collected during the platform studies. Due to fluctuations in the availability of horses and mules, it was not possible to collect in the same area throughout the entire year. This has undoubtedly influenced the data, since highly localized differences in species composition and size of the tabanid populations are thought to occur. Usually two eleven-period collections were made per month; however for October there was only one, for April and June there were 3, and for May there were four collections. Three day-long collections and several 3-5 hour collections were made in July.

The diurnal biting activity and seasonal distribution of the six most common tabanids attracted to the horses and mules is presented in Tables II-56, II-57. There was considerable variability among the different species as to the time a peak in their biting activity occurred (Table II-56). Stypommodica had the earliest peak, which occurred from approximately 1200 to 1300 hours, while Stypommodica pequeniensis had the latest peak which occurred from approximately 1700 to 1800 hours. Both species of Stypommodica and both species of Leucotabanus attained their maximum population size in April (Table II-62). Adults of Poeciloderas quadripunctatus var. amabilinus appeared to have a peak level of abundance in January and February, a time at which most other species are either not present or are present only in small numbers. Monthly fluctuations in biting activity are least pronounced for this species.

Table II-56. Comparative diurnal temporal distribution of biting activity of six species of Tabanidae.^{1/}

Period beginning ^{2/}	07	08	09	10	11	12	13	14	15	16	17
Periods/Level	24	30	32	32	32	22	28	29	30	30	29
<u>Dichelacera chocoensis</u>											
No. Collected	34	59	138	158	164	157	373	762	700	846	603
No./Period	1.41	1.96	4.31	4.93	5.12	7.13	13.32	26.27	23.33	28.20	20.79
<u>Poeciloderas quadripunctatus</u> var. <u>amabilinus</u>											
No. Collected	4	6	10	16	24	24	38	25	22	11	4
No./Period	0.16	0.20	0.31	0.50	0.75	1.09	1.35	0.86	0.73	0.36	0.13
<u>Stypommisa pequeniensis</u>											
No. Collected	5	4	10	6	5	4	11	24	76	147	199
No./Period	0.21	0.13	0.31	0.19	0.16	0.18	0.39	0.83	2.53	4.90	6.86
<u>Stypommisa modica</u>											
No. Collected	0	6	19	22	19	31	22	23	9	14	9
No./Period	0	0.20	0.59	0.68	0.59	1.40	0.78	0.79	0.30	0.46	0.31
<u>Leucotabanus flavinotum</u>											
No. Collected	1	0	2	1	3	1	4	23	31	83	26
No./Period	0.04	0	0.06	0.03	0.09	0.04	0.14	0.79	1.03	2.76	0.89
<u>Leucotabanus exaestuans</u>											
No. Collected	4	2	5	4	6	13	34	34	51	36	9
No./Period	0.16	0.06	0.15	0.12	0.18	0.59	1.21	0.17	1.70	1.20	0.31

^{1/} Based on collections from two horses or mules at forest edge sites.^{2/} The time between sunrise and sunset is divided into 12 equal periods; the hour designations approximate the beginning of each period which varies with day length throughout the year. Periods with heavy rain, which prevented collecting, are excluded. The first day period is excluded.

Table II-57. Seasonal distribution of six species of Tabanidae.^{1/}

Periods/level	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
<i>Dichelacera chocoensis</i>												
No. Collected	0	0	0	8	285	1001	1677	533	351	32	105	2
No./Period	0	0	0	0.24	6.47	30.33	33.54	22.20	18.47	3.20	5.25	0.09
<i>Peciloderas quadripunctatus</i> var. <i>amabilinus</i>												
No. Collected	23	40	6	15	19	25	23	5	14	1	7	6
No./Period	1.09	1.81	0.28	0.45	0.43	0.75	0.46	0.20	0.73	0.10	0.35	0.28
<i>Stypommisa pequeniensis</i>												
No. Collected	0	0	2	118	144	101	77	30	16	3	0	0
No./Period	0	0	0.10	3.58	3.27	3.06	1.54	1.25	0.84	0.30	0	0
<i>Stypommisa modica</i>												
No. Collected	1	5	37	85	11	13	2	14	6	0	0	0
No./Period	0.04	0.22	1.76	2.57	0.25	0.39	0.04	0.58	0.31	0	0	0
<i>Leucotabanus flavinotum</i>												
No. Collected	0	4	2	73	20	20	42	9	4	1	0	0
No./Period	0	0.18	0.09	2.21	0.45	0.60	0.84	0.37	0.21	0.10	0	0
<i>Leucotabanus exaestuans</i>												
No. Collected	3	15	6	56	48	18	40	6	2	1	1	2
No./Period	0.14	0.68	0.28	1.69	1.09	0.54	0.80	0.25	0.10	0.10	0.05	0.09

^{1/} Based on collections from two horses or mules at forest edge sites from July 1970 through July 1971.

RESULTS

By far, the most abundant biting group in the clearing habitat were the Simuliidae. Since large numbers of the two species of blackflies, Simulium metallicum Bellardi and S. exiguum Roubaud were collected, it is possible to examine the relationships between the different sites statistically. This was done by means of correlating each site against each other in average numbers caught per collection period on a monthly basis. This tells us which sites are subject to the same influences determining seasonal abundance of blackflies biting man (Table II-58).

Using the same technique to compare daily averages for sites collected simultaneously (Sites A, B, and D together; sites C, E, and F together), it is possible to correlate daily activity fluctuations. The biting activity of S. metallicum was greatest during the first catch period, approximately from 0700 to 0800 hrs. The mean catch declined noticeably through the third period, and remained relatively constant thereafter (Fig. II-30). In contrast, the biting activity of S. exiguum was less, but variable, throughout the collecting periods (Fig. II-31). Interestingly, S. exiguum was infrequently collected from bench site D.

If we assume that the data in Table II-58 represent correlation of seasonal activity and the data in Table II-59 represent correlation of daily activity, then for Simulium metallicum Bellardi, site A acts most independently of the other sites with respect to both seasonal and daily variation. Similarly, we can conclude that site C is most representative of all sites. With respect to S. exiguum Roubaud, site F is most dissimilar to the others with respect to seasonal variation while site A varies most independently on a daily basis. Again for S. exiguum, site C is most representative of all sites.

The same analysis was applied to relate rainfall levels taken at the Providencia electrical plant to monthly activity of both Simulium species.

Table II-58. Correlation of average hourly catch per month
between clearing sites.

Site Combination	Degrees of Freedom	Correlation Coefficient	
		<u>Simulium metallicum</u>	<u>Simulium exiguum</u>
A x B	9	0.524 NS	0.833 **
A x C	9	0.688 *	0.761 **
A x D	9	0.686 *	0.676 *
A x E	8	0.867 **	0.777 **
A x F	8	0.450 NS	0.623 NS
B x C	9	0.859 **	0.900 **
B x D	9	0.887 **	0.878 **
B x E	8	0.765 **	0.514 NS
B x F	8	0.911 **	0.257 NS
C x D	9	0.764 **	0.984 **
C x E	8	0.889 **	0.798 **
C x F	8	0.927 **	0.828 **
D x E	8	0.746 *	0.642 *
D x F	8	0.790 **	0.661 *
E x F	8	0.740 *	0.875 **

NS - Not Significant * - Significant at 5% level ** - Significant
at 1% level

Table II- 59 Correlation of average hourly catch per day between sites.

Site Combination	Degrees of Freedom	Correlation Coefficient	
		<u>Simulium metallicum</u>	<u>Simulium exiguum</u>
A x B	31	0.360 *	0.292 NS
A x D	31	0.417 *	0.136 NS
B x D	31	0.570 **	0.601 **
C x E	29	0.605 **	0.626 **
C x F	29	0.687 **	0.564 **
E x F	30	0.583 **	0.552 **

NS - Not Significant * - Significant at 5% level ** - Significant at 1% level

Simulium metallicum Bellardi

A ——— D - - - -
 B ——— E - - - -
 C - - - - F - - - -
 STATION

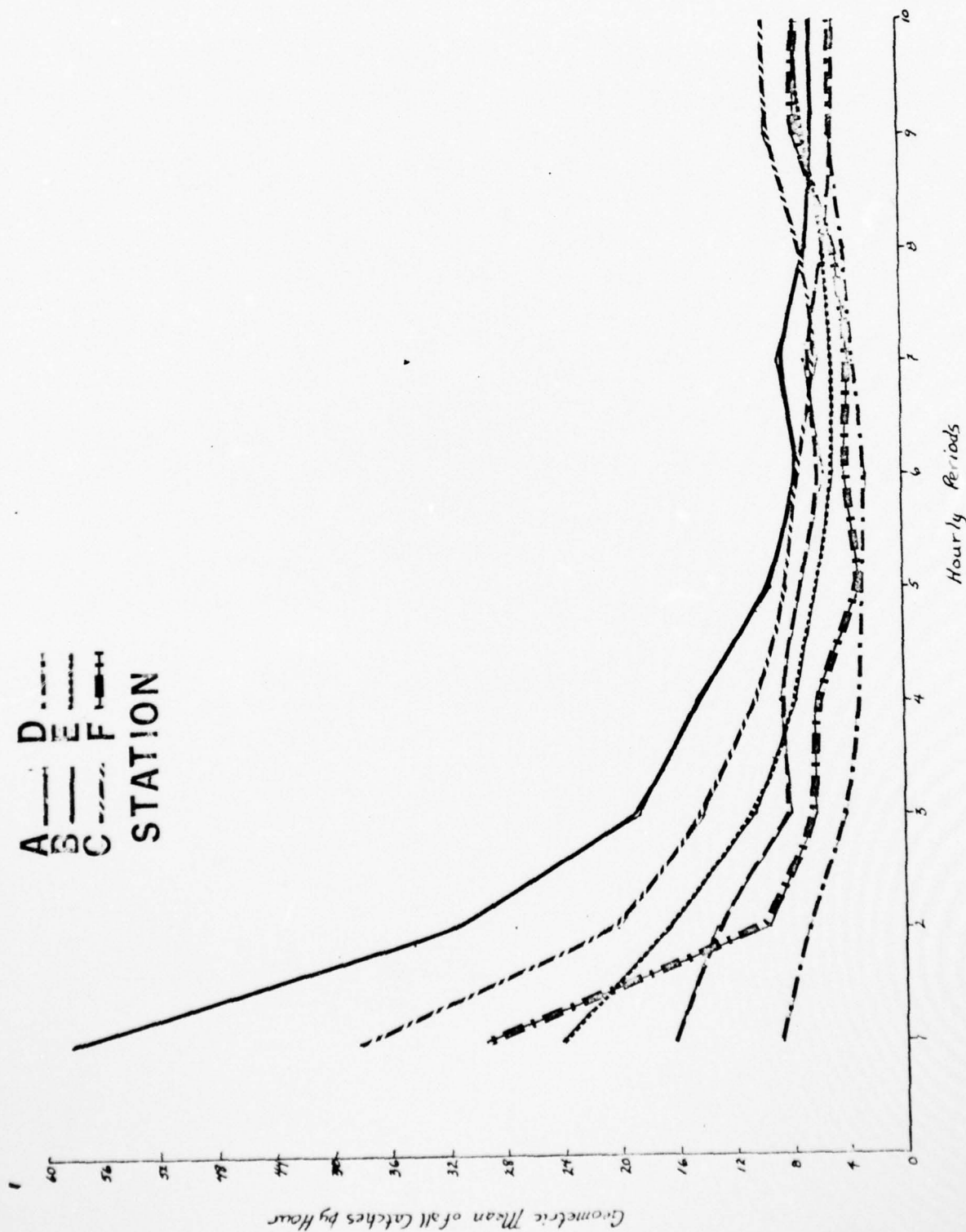


Fig. II-30. Temporal patterns of man-biting activity at six clearing sites by *S. metallicum* based on geometric means.

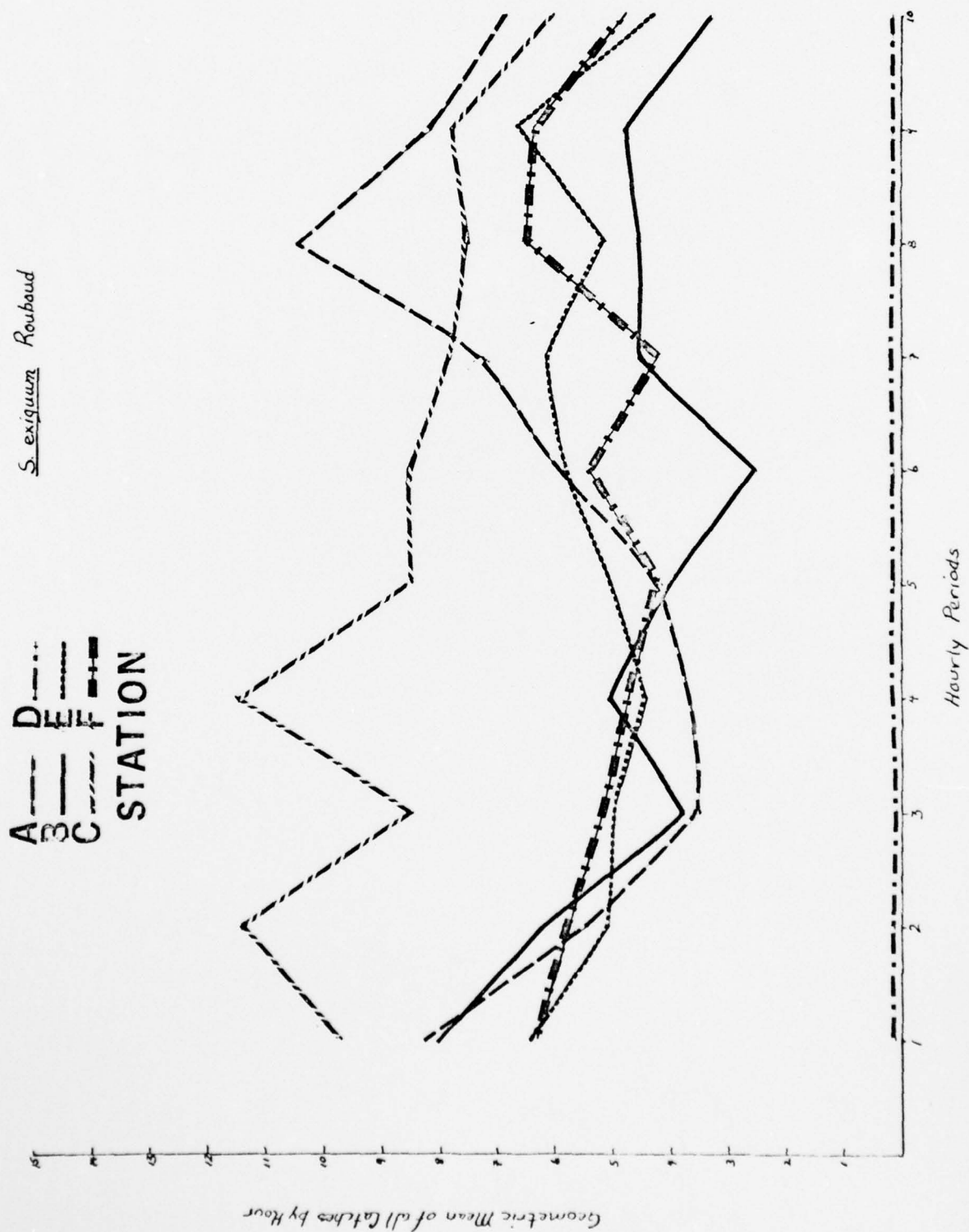


Fig. II-31. Temporal patterns of man-biting activity at six clearing sites by *S. exiguum* based on geometric means.

This was done by matching hourly average catches per month first with the rainfall of the same month (month 0), then with the previous month (month -1), then with that of two months earlier (month -2), and finally the rainfall three months previous (month -3). Although no significant correlation could be found between these data for S. metallicum Bellardi, significant correlation was found for S. exiguum Roubaud at all sites at either month -2 or month -3 (Table II-60).

This correlation indicates that conditions favorable for a large larval population produce adult peak populations (as indicated by catch) in 2 -3 months, after which the catch again drops. One possible conclusion is that it takes the population this long to reach carrying capacity. Since the generation time for this species is about 18-20 days (Dalmat 1955) this lag seems to be approximately three generations.

Presently, a final statistical procedure is being applied to the data. In attempt to examine population diversity at a closer level, generic diversity indices are being computed for each collection day at each site. Cameron (1972) found that diversity indices relate directly to resource availability. Thus, trends in diversity may indicate trends in resource levels throughout the year.

The ideas presented in this discussion were necessarily not definitive. Some of the data seems to yield conflicting information upon analysis and until closer examination is made, it is difficult to give definite information concerning site interrelations and monthly and daily activity levels. Definite conclusions concerning the general ecology of cleared sections of rainforest and their effects on hematophagous insect populations require additional study.

Table II-60. Correlation of rainfall with monthly biting activity of
Simulium exiguum Roubaud.

Month	Site A	Site B	Site C	Site D	Site E	Site F
0	0.541	0.318	0.295	0.134	0.533	0.488
-1	0.162	0.417	0.547	0.525	0.174	0.000
-2	0.652**	0.856*	0.909*	0.949*	0.301	0.290
-3	0.336	0.030	0.235	0.200	0.642*	0.822*

* Significant at 5% level, ** Significant at 1% level.

Within the forest the biting activity of the black fly, Simulium metallicum appeared to be of greatest intensity in the canopy (Tables II-61, II-62). This preference was most pronounced at the Providencia site, which was also the area where this species was most abundant (Table II-62). The biting activity of S. metallicum at the Buenos Aires I site appears to have been greatest at ground level, and at the Buenos Aires II site this blackfly occurred in almost equal numbers at ground level in the canopy. The summary of temporal distribution shows that biting activity peaked in the catch period beginning at 0700 hours and declined abruptly during the following catch period followed by a descent to about 1300 hours (Tables II-61, II-63). A similar pattern occurred in the canopy but after catch period 13 there was an increase in biting activity again which reached a second peak at approximately 1700 hours. At ground level the biting activity of S. metallicum was most pronounced from 0900 to 1200 hours and is very low after 1500 hours. This species was never observed biting in the forest after sunset. Considerable variations in the time of maximum biting activity existed between the platform sites. The Providencia site had a temporal distribution very similar to that already described for the canopy, while no distinct peak of activity was evident at the Buenos Aires I site. The seasonal distribution of biting activity suggests that the population level of S. metallicum attained a pronounced peak in April and May (Table II-64). However, the high rate of biting activity observed in April may be unusual, since it could have been produced by the abnormally high March rainfall.

Table II-6 L. Simulium metallicum diurnal temporal and vertical patterns of biting activity in the forest.

Period beginning*	07	08	09	10	11	12	13	14	15	16	17	sunset		Totals† (%)
												18	18	
No./Period	52	56	58	58	58	57	57	57	57	50	34	33		
Ground Level														
No. Taken	26	33	48	57	52	50	36	36	15	8	3	0	0	364
No./Period	0.50	0.59	0.83	0.98	0.90	0.88	0.63	0.63	0.26	0.16	0.08	0	0	0.61 (26)
Understory Level														
No. Taken	37	27	37	33	18	25	15	15	15	7	2	0	0	231
No./Period	0.71	0.48	0.64	0.57	0.31	0.44	0.26	0.26	0.26	0.14	0.05	0	0	0.38 (16)
Canopy Level														
No. Taken	232	119	85	63	48	35	24	35	39	58	68	0	0	806
No./Period	4.46	2.12	1.46	1.09	0.83	0.61	0.42	0.61	0.68	1.16	2.00	0	0	1.35 (58)
Total														
No. Taken	295	179	170	153	118	110	75	86	69	73	73	0	0	
No./Period	1.89	1.06	0.97	0.87	0.67	0.64	0.43	0.50	0.40	0.48	0.71	0	0	

* The time between sunrise and sunset divided into 12 equal periods; the hour designations approximate the beginning of each period which varies with day length throughout the year. Periods with heavy rain which prevented collecting are excluded. The first day period is excluded and the first night period is included.

† Catch period 18 excluded

Table II-62. Vertical distribution of Simulium metallicum
at four forest collecting sites.

	No. Taken	No./Period	%
Buenos Aires I			
Ground level	101	0.74	48
Understory	31	0.23	15
Canopy	77	0.57	37
Buenos Aires II			
Ground level	54	0.40	40
Understory	28	0.21	21
Canopy	52	0.38	39
Providencia			
Ground level	198	1.20	20
Understory	144	0.87	15
Canopy	627	3.82	65
Tiroteos			
Ground level	11	0.07	12
Understory	28	0.17	32
Canopy	50	0.32	56

Table II-63. Temporal distribution of Simulium metallicum biting activity at different sites.

Period beginning	07	08	09	10	11	12	13	14	15	16	17	Totals
Buenos Aires I												
No. Taken	8	11	21	23	25	29	23	29	16	22	2	209
No. Periods	27	36	39	39	39	36	39	39	39	36	39	408
No./Period	0.30	0.30	0.54	0.59	0.64	0.80	0.59	0.74	0.41	0.61	0.05	0.51
Buenos Aires II												
No. Taken	7	11	12	35	20	14	17	9	7	2		134
No. Periods	39	39	42	42	42	42	42	42	42	39		408
No./Period	0.18	0.28	0.28	0.83	0.48	0.33	0.40	0.21	0.17	0.05		0.32
Providencia												
No. Taken	247	148	122	87	67	54	28	38	38	48	65	969
No. Periods	45	48	48	48	48	48	45	45	45	39	33	492
No./Period	6.09	3.08	2.54	1.81	1.40	1.12	0.62	0.84	0.84	1.23	1.96	2.37
Tiroteos												
No. Taken	6	9	15	8	6	13	7	10	8	1	6	89
No. Periods	45	45	45	45	45	45	45	45	45	39	30	474
No./Period	0.13	0.20	0.33	0.18	0.13	0.29	0.16	0.22	0.18	0.02	0.20	0.18

Table II-64. Seasonal distribution of Simulium metallicum biting activity.

	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
No. Taken	77	106	62	278	281	173	106	94	43	46	26	109
No. Periods [*]	129	159	156	156	204	177	189	114	126	123	120	129
No./Period	0.59	0.66	0.39	1.78	1.37	0.97	0.56	0.82	0.34	0.37	0.21	0.84

* Catch period 18 excluded

AD-A049 853

WISCONSIN UNIV MADISON DEPT OF VETERINARY SCIENCE F/G 6/3
ECOLOGICAL AND AEROSPACE MEDICAL ASPECTS OF VIRUS DISEASES. PAR--ETC(U)
OCT 74 R P HANSON, T M YUILL AFOSR-72-2337

UNCLASSIFIED

AFOSR-TR-75-1645-REV

NL

4 of 4

ADAD49 853



END
DATE
FILMED
3 -78
DDC

RESULTS

The most abundant man-biting mosquito in the forested areas of the Providencia region was Haemagogus capricorni falco. A total of 1425 specimens of this species were captured during the platform studies. The very high biting activity of this species at the Tiroteos site compared to the other sites (Tables II-65, II-66) raises several interesting questions concerning the relative abundance in relation to forest physiognomy and floristics. The observed vertical distribution of this species (Tables II-66, II-67) conforms with its well established preference for the canopy. The biting activity of H. capricorni falco in the canopy was most pronounced at the Tiroteos and Providencia platform sites and was considerably less well defined at the Buenos Aires II site, which might be due to the reduced height of the platform at this site. The biting activity of H. capricorni falco was most intense from approximately 1100 to 1500 hours (Tables II-65, II-67). It is interesting to note that the mean hourly forest temperature curve (Table II-4) began to descend at 1500 hours. The peak of biting activity for all three levels occurred during the catch period beginning at 1200 hours. The seasonal distribution of biting activity (Table II-68) indicates that the population of this species was lowest during the dry season but was not drastically reduced. However a distinct dry season did not occur in 1970. The population apparently peaked in May and June and there is some indication that it then stabilized at a reduced rate for the rest of the year. The low number per period for September is thought to be at least partially due to the fact that no collections were made during this month at the Tiroteos site while two were made at the Buenos Aires II

Table II-65 Temporal distribution of Haemagogus capricorni falco biting activity at different forest sites.

Period beginning	07	08	09	10	11	12	13	14	15	16	17	Totals
Buenos Aires I												
No. Taken	0	0	4	15	27	38	30	28	32	13	1	188
No. Periods	27	33	33	33	33	31	33	33	33	30	39	360
No./Period	0	0	0.12	0.46	0.82	1.23	0.91	0.85	0.97	0.43	0.03	0.52
Buenos Aires II												
No. Taken	1	1	8	14	21	23	15	15	12	6		116
No. Periods	39	39	39	39	39	39	39	39	39	33		384
No./Period	0.03	0.03	0.21	0.36	0.54	0.59	0.38	0.38	0.31	0.18		0.30
Providencia												
No. Taken	4	6	9	18	21	33	21	41	29	8	3	193
No. Periods	39	42	42	42	42	42	42	42	42	36	33	444
No./Period	0.10	0.14	0.21	0.43	0.50	0.79	0.50	0.98	0.69	0.22	0.09	0.43
Tiroteos												
No. Taken	1	5	29	105	149	167	184	160	93	28	7	928
No. Periods	45	45	45	45	45	45	45	45	45	39	30	474
No./Period	0.02	0.11	0.64	2.33	3.31	3.71	4.09	3.56	2.07	0.72	0.23	1.96

Table II-66. Vertical distribution of Haemagogus capricorni falco
at four forest collecting sites.

	No. Taken	No./Period	%
Buenos Aires I			
Ground level	23	0.19	12
Understory	58	0.49	31
Canopy	107	0.91	57
Buenos Aires II			
Ground level	22	0.17	19
Understory	38	0.30	33
Canopy	56	0.44	48
Providencia			
Ground level	2	0.01	1
Understory	43	0.29	22
Canopy	148	1.00	77
Tiroteos			
Ground level	10	0.06	1
Understory	193	1.22	21
Canopy	725	4.59	78

Table II-67. Haemagogus capricorni falco diurnal temporal and vertical patterns of biting activity.

Period beginning*	07	08	09	10	11	12	13	14	15	16	17	sunset		Totals ⁺ (%)
												18	18	
Periods/Level	50	53	53	53	53	53	53	53	53	46	34	33	33	
Ground Level														
No. Taken	0	0	3	9	9	13	9	8	5	0	1	0	0	57
No./Period	0	0	0.06	0.17	0.17	0.24	0.17	0.15	0.09	0	0.03	0	0	0.10 (4)
Understory Level														
No. Taken	3	3	12	31	47	63	57	70	33	12	1	0	0	332
No./Period	0.06	0.06	0.23	0.55	0.98	1.19	1.08	1.32	0.62	0.26	0.03	0	0	0.60 (23)
Canopy Level														
No. Taken	3	9	35	112	162	185	184	166	128	43	9	0	0	1036
No./Period	0.06	0.17	0.66	2.11	3.06	3.49	3.47	3.13	2.42	0.94	0.26	0	0	1.87 (73)
Total														
No. Taken	6	12	50	152	218	261	250	244	166	55	11	0	0	
No./Period	0.04	0.08	0.31	0.96	1.37	1.64	1.57	1.53	1.04	0.40	0.11	0	0	

* The time between sunrise and sunset divided into 12 equal periods; the hour designations approximate the beginning of each period which varies with day length throughout the year. Periods with heavy rain which prevented collecting are excluded. The first day period is excluded and the first night period is included.

+ Catch period 18 excluded.

Table II-68 Seasonal distribution of Haemagogus capricorni falco collections.

	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
No. Taken	44	63	50	186	223	229	139	77	35	136	76	97
No. Periods*	129	159	156	156	156	159	159	90	126	123	120	129
No./Period	0.34	0.40	0.32	1.19	1.43	1.88	0.87	0.86	0.28	1.11	0.63	0.75

* Catch period 18 excluded

site. Conversely, the relatively high number per period for October may reflect the fact that two collections were made at the Tiroteos site.

The forest platform studies indicate that Haemagogus clarki (Tables II-69 to II-72) occurred at a comparatively small population level and exhibited a very spotty distribution in the Providencia region. A disproportionately large number of specimens were collected at the Tiroteos site, while very few were taken at either of the Buenos Aires sites (Table II-69). The biting activity of this species was greatest from 1000 to 1500 hours (Table II-69). Although the peak of biting activity occurs at the same time in the understory as in the canopy, the period of biting activity in the understory was of shorter duration than in the canopy (Table II-71). A majority of these mosquitoes were captured in the canopy but a considerable amount of biting activity also occurred in the understory. The seasonal pattern of distribution for H. clarki was rather poorly defined. (Table II-72). The two peaks in biting activity, June and October, follow months which had over 20 inches of rain. The comparatively large difference between September and October may again be due to the fact that no collections were made in September at the Tiroteos site.

Sabethes chloropterus did not appear to have a distinct peak in biting activity but rather tends to have had a broad and somewhat uniform period of maximum activity extending from 0900 to 1700 hours (Tables II-73, II-74). However, in the canopy there appeared to be a small peak in biting activity from approximately 1200 to 1500 hours (Table II-74). This species showed a strong preference for the canopy but the percentage taken at this level varies considerably between sites (Table II-75). S. chloropterus was distinctly more abundant at the Providencia and Tiroteos sites. This species appeared

Table II-69. Temporal distribution of Haemagogus clarki biting activity at different sites.

Period beginning	07	08	09	10	11	12	13	14	15	16	17	Totals
Buenos Aires I												
No. Taken	0	0	1	1	3	3	2	5	0	1	0	16
No. Periods	27	36	39	39	39	36	39	39	39	36	0	369
No./Period	0	0	0.02	0.02	0.08	0.08	0.05	0.13	0	0.03	0	0.04
Buenos Aires II												
No. Taken	0	0	1	2	1	1	1	0	0	1	7	7
No. Periods	39	39	42	42	42	42	42	42	42	36	408	408
No./Period	0	0	0.02	0.05	0.02	0.02	0.02	0	0	0.03	0.01	0.01
Providencia												
No. Taken	2	4	5	14	4	6	6	5	6	0	52	52
No. Periods	45	48	48	48	48	48	45	45	45	39	459	459
No./Period	0.04	0.08	0.10	0.29	0.08	0.12	0.13	0.11	0.13	0	0.11	0.11
Tiroteos												
No. Taken	2	6	14	19	23	29	20	19	8	5	145	145
No. Periods	45	45	45	45	45	45	45	45	45	39	444	444
No./Period	0.04	0.13	0.31	0.42	0.51	0.64	0.44	0.42	0.18	0.13	0.32	0.32

Table II-70. Vertical distribution of Haemagogus clarki at four forest collecting sites.

	No. Taken	No./Period	%
Buenos Aires I			
Ground level	2	0.02	13
Understory	5	0.04	31
Canopy	9	0.07	56
Buenos Aires II			
Ground level	3	0.02	43
Understory	2	0.01	29
Canopy	2	0.01	28
Providencia			
Ground level	3	0.02	6
Understory	19	0.12	37
Canopy	30	0.20	57
Tiroteos			
Ground level	4	0.03	3
Understory	60	0.40	41
Canopy	81	0.55	56

Table II-71. Haemagogus clarki diurnal temporal and vertical patterns of biting activity.

Period beginning*	07	08	09	10	11	12	13	14	15	16	17	Total ⁺ (%)
No. Periods	52	56	58	58	58	57	57	57	57	50	34	
Ground Level												
No. Taken	0	1	1	2	3	1	0	2	1	1	0	12
No./Period	0	0.02	0.02	0.03	0.05	0.02	0	0.04	0.02	0.02	0	0.02 (6)
Understory Level												
No. Taken	0	1	6	17	11	20	13	13	3	2	0	86
No./Period	0	0.02	0.10	0.29	0.19	0.35	0.23	0.29	0.05	0.04	0	0.15 (39)
Canopy Level												
No. Taken	4	8	14	17	17	18	16	14	10	4	0	122
No./Period	0.08	0.14	0.24	0.29	0.29	0.32	0.28	0.24	0.18	0.08	0	0.22 (55)
Total												
No. Taken	4	10	21	36	31	39	29	29	14	7	0	
No./Period	0.02	0.06	0.12	0.21	0.18	0.23	0.17	0.17	0.08	0.05	0	

* The time between sunrise and sunset divided into 12 equal periods; the hour designations approximate the beginning of each period which varies with day length throughout the year. Periods with heavy rain which prevented collecting are excluded. The first day period is excluded.

+ Catch period 17 excluded

Table II-72. Seasonal distribution of Haemagogus clarki biting collections.

	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
No. Taken	13	12	4	14	16	40	20	14	12	42	17	16
No. Periods*	120	150	147	147	195	168	174	108	120	117	114	120
No./Period	0.11	0.08	0.03	0.10	0.08	0.24	0.11	0.13	0.10	0.36	0.15	0.13

* Catch period 18 excluded

Table II-73 Temporal distribution of Sabethes chloropterus biting activity at different sites.

Period beginning	07	08	09	10	11	12	13	14	15	16	17	Totals
Buenos Aires I												
No. Taken	2	1	7	7	10	5	8	13	10	5	3	70
No. Periods	27	36	39	39	39	36	39	39	39	36	39	408
No./Period	0.07	0.03	0.18	0.15	0.26	0.14	0.20	0.33	0.26	0.14	0.08	0.17
Buenos Aires II												
No. Taken	0	2	9	6	6	2	7	8	5	4		49
No. Periods	39	39	42	42	42	42	42	42	42	36		408
No./Period	0	0.05	0.21	0.14	0.14	0.05	0.17	0.19	0.12	0.11		0.12
Providencia												
No. Taken	4	12	27	18	26	29	35	25	18	17	8	219
No. Periods	45	48	48	48	48	48	45	45	45	39	33	492
No./Period	0.09	0.25	0.56	0.38	0.54	0.60	0.78	0.56	0.40	0.44	0.24	0.44
Tiroteos												
No. Taken	7	13	16	16	28	24	19	29	22	17	7	198
No. Periods	45	45	45	45	45	45	45	45	45	39	30	474
No./Period	0.16	0.29	0.36	0.36	0.62	0.53	0.42	0.64	0.49	0.44	0.23	0.42

Table II-74. Sabethes chloropterus diurnal temporal and vertical patterns of biting activity.

Period beginning*	07	08	09	10	11	12	13	14	15	16	17	sunset		Totals ⁺ (%)
												18	18	
No. Periods	52	56	58	58	58	57	57	57	57	50	34	33	33	
Ground Level														
No. Taken	0	2	3	1	1	2	3	2	0	0	1	0	0	15
No./Period	0	0.04	0.05	0.02	0.02	0.04	0.05	0.04	0	0	0.03	0	0	0.03 (3)
Understory Level														
No. Taken	3	3	14	17	28	16	16	24	11	8	0	0	0	140
No./Period	0.06	0.05	0.24	0.29	0.48	0.28	0.28	0.42	0.19	0.16	0	0	0	0.24 (26)
Canopy Level														
No. Taken	10	23	42	28	41	42	50	49	44	35	17	0	0	381
No./Period	0.19	0.39	0.72	0.48	0.71	0.74	0.88	0.86	0.77	0.70	0.50	0	0	0.64 (71)
Total														
No. Taken	13	28	59	46	70	60	69	75	55	43	18	0	0	
No./Period	0.08	0.17	0.34	0.26	0.40	0.35	0.40	0.44	0.32	0.29	0.18	0	0	

* The time between sunrise and sunset divided into 12 equal periods; the hour designations approximate the beginning of each period which varies with day length throughout the year. Periods with heavy rain which prevented collecting are excluded. The first day period is excluded and the first night period is included.

+ Catch period 18 excluded

Table II-75. Vertical distribution of Sabethes chloropterus
at four forest collecting sites.

	No. Taken	No./Period	%
Buenos Aires I			
Ground level	6	0.04	9
Understory	25	0.18	36
Canopy	39	0.29	35
Buenos Aires II			
Ground level	2	0.02	4
Understory	13	0.10	27
Canopy	34	0.25	69
Providencia			
Ground level	1	0.01	> 1
Understory	44	0.27	20
Canopy	174	1.06	79
Tiroteos			
Ground level	6	0.04	3
Understory	58	0.37	29
Canopy	134	0.85	68

to have a remarkably uniform seasonal distribution (Table II-76 but whether this would also be true for years with a distinct dry season is not known.

The temporal distribution of Sabethes belisarioi indicates that this species remained relatively inactive until about 1000 hours and had a comparatively narrow range of maximum biting activity from approximately 1200 to 1500 hours (Tables II-77, II-78). This species was most abundant at the Providencia and Buenos Aires I sites and had a very pronounced preference for the canopy (Table II-79). It rarely occurred near the forest floor. The considerably greater number of individuals taken at the Buenos Aires I site compared to the Buenos Aires II site suggests that the upper platform at the latter site may not have been sufficiently high to adequately sample this species. The seasonal distribution of biting activity (Table II-80) indicated that S. belisarioi may have had a distinct seasonal fluctuation in population size. An increased population level occurred from June through October and had a peak in September.

The preceding mosquitoes are all arboreal species which are dependent upon the forest habitat for their survival since their larval stages were restricted to various kinds of container habitats located in or near the canopy. However, the larvae of Psorophora albipes develop in transient ground pools, and thus this species was not as directly dependent upon the forest for survival. As one might then expect, P. albipes did not have the preference exhibited by the other mosquitoes for the canopy (Tables II-81, II-82). The vertical distribution of biting activity showed that there is a slight preference for the ground level, with a nearly equal level of activity occurring in both the understory and the canopy. The preference for the ground level was most pronounced at the Buenos Aires I and Tiroteos

Table IF-76- Seasonal distribution of Sabethes chloropterus biting collections.

	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
No. Taken	36	58	45	33	50	61	63	43	30	50	33	34
No. Periods*	129	159	156	156	204	177	189	114	126	123	120	129
No./Period	0.28	0.36	0.29	0.21	0.24	0.34	0.33	0.38	0.24	0.41	0.28	0.26

* Catch period 18 excluded

Table II-77. Temporal distribution of Sabethes bellisariol biting activity at different sites.

Period beginning	07	08	09	10	11	12	13	14	15	16	17	Totals
Buenos Aires I												
No. Taken	1	0	5	6	13	16	15	31	9	1	4	101
No. Periods	27	36	39	39	39	36	39	39	39	36	39	408
No./Period	0.04	0	0.13	0.15	0.33	0.44	0.38	0.80	0.23	0.03	0.10	0.25
Buenos Aires II												
No. Taken	1	0	0	5	2	7	7	6	5	3		36
No. Periods	39	39	42	42	42	42	42	42	42	36		408
No./Period	0.03	0	0	0.12	0.05	0.17	0.17	0.14	0.12	0.08		0.09
Providencia												
No. Taken	0	4	7	16	18	25	19	30	20	3	1	143
No. Periods	45	48	48	48	48	48	45	45	45	39	33	492
No./Period	0	0.08	0.15	0.33	0.38	0.52	0.42	0.67	0.44	0.08	0.03	0.29
Tiroteos												
No. Taken	0	1	4	9	18	15	15	14	8	2	1	87
No. Periods	45	45	45	45	45	45	45	45	45	39	30	474
No./Period	0	0.02	0.09	0.20	0.40	0.33	0.33	0.31	0.18	0.05	0.03	0.18

Table II-78. Sabethes belisariol diurnal temporal and vertical patterns of biting activity.

Period beginning*	07	08	09	10	11	12	13	14	15	16	17	18	sunset	Totals ⁺ (%)
No. Periods	52	56	58	58	58	57	57	57	57	50	34	33		
Ground Level														
No. Taken	0	0	0	2	0	0	0	0	0	0	0	0	2	
No./Period	0	0	0	0.03	0	0	0	0	0	0	0	0	0.00	(1)
Understory Level														
No. Taken	0	0	3	7	5	10	5	13	6	1	1	0	51	
No./Period	0	0	0.05	0.12	0.09	0.18	0.09	0.23	0.10	0.02	0.03	0	0.09	(14)
Canopy Level														
No. Taken	2	5	13	27	46	53	51	68	36	8	5	0	314	
No./Period	0.04	0.09	0.22	0.47	0.79	0.93	0.90	1.19	0.63	0.16	0.15	0	0.53	(85)
Total														
No. Taken	2	5	16	36	51	63	56	81	42	9	6	0		
No./Period	0.01	0.03	0.09	0.21	0.29	0.37	0.33	0.47	0.24	0.06	0.06	0		

* The time between sunrise and sunset divided into 12 equal periods; the hour designations approximate the beginning of each period which varies with day length throughout the year. Periods with heavy rain which prevented collecting are excluded. The first day period is excluded and the first night period is included.

+ Catch period 18 excluded.

Table II-79. Vertical distribution of Sabethes belisarioi
at four forest collecting sites.

	No. Taken	No./Period	%
Buenos Aires I			
Ground level	1	0.01	1
Understory	22	0.16	22
Canopy	78	0.57	77
Buenos Aires II			
Ground level	0	0	0
Understory	5	0.04	14
Canopy	31	0.23	86
Providencia			
Ground level	1	0.01	1
Understory	11	0.07	8
Canopy	131	0.80	91
Tiroteos			
Ground level	0	0	0
Understory	13	0.08	15
Canopy	74	0.47	85

Table II-80. Seasonal distribution of Sabethes belisarioi biting collections.

	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
No. Taken	25	20	15	26	22	50	54	30	57	28	20	20
No. Periods*	129	159	156	156	204	177	189	114	126	123	120	129
No./Period	0.19	0.13	0.10	0.17	0.11	0.28	0.29	0.26	0.45	0.23	0.17	0.16

* Catch period 18 excluded

Table II-81. Vertical distribution of Psorophora albipes
at four forest collecting sites.

	No. Taken	No./Period	%
Buenos Aires I			
Ground level	48	0.19	45
Understory	28	0.11	27
Canopy	30	0.12	28
Buenos Aires II			
Ground level	138	1.01	36
Understory	120	0.88	31
Canopy	129	0.95	33
Providencia			
Ground level	32	0.12	36
Understory	26	0.10	30
Canopy	30	0.11	34
Tiroteos			
Ground level	111	0.44	44
Understory	87	0.34	34
Canopy	57	0.22	22

Table II-82. Psorophorus albipes temporal and vertical patterns of biting activity.

Period beginning *	Periods/ Level	Number taken/Number per period			Total
		Ground Level	Understory Level	Canopy Level	
01	22	0/0	0/0	0/0	0/0
02	23	0/0	1/0.04	0/0	1/0.01
03	21	1/0.05	1/0.05	1/0.05	3/0.05
04	22	1/0.04	1/0.04	1/0.04	3/0.04
05	26	2/0.10	1/0.05	1/0.05	4/0.07
06 sunrise	--	-/-	-/-	-/-	-/-
07	52	45/0.86	20/0.38	20/0.38	85/0.45
08	56	24/0.43	21/0.38	25/0.45	70/0.42
09	58	25/0.43	16/0.28	13/0.22	54/0.31
10	58	27/0.46	22/0.38	23/0.40	72/0.41
11	58	28/0.48	26/0.45	23/0.40	77/0.44
12	57	17/0.31	28/0.49	21/0.37	66/0.39
13	57	28/0.49	34/0.60	21/0.37	83/0.48
14	57	45/0.79	29/0.51	27/0.47	101/0.59
15	57	47/0.82	42/0.74	29/0.51	118/0.69
16	50	19/0.38	12/0.24	18/0.36	49/0.33
17	34	16/0.47	6/0.18	15/0.44	37/0.36
18 sunset	33	3/0.09	0/0	4/0.12	7/0.07
19	30	1/0.03	1/0.03	1/0.03	3/0.03
20	32	0/0	0/0	0/0	0/0
21	32	0/0	0/0	1/0.03	1/0.01
22	30	0/0	0/0	0/0	0/0
23	29	0/0	0/0	1/0.03	1/0.01
24	27	0/0	0/0	1/0.04	1/0.01
Total (%)		329/0.36 (39)	261/0.28 (31)	246/0.27 (30)	

* The time between sunrise and sunset is divided into 12 equal periods and the time between sunset and sunrise is divided into 12 equal periods. The hour designations approximate the beginning of each period which varies with day length throughout the year. Periods with heavy rain which prevented collecting are excluded. Catch period beginning 06 was not studied.

sites (Table II-81). P. albipes was primarily diurnal with only an occasional individual biting during the night. There appeared to be a small peak in biting activity from approximately 1400 to 1600 hours (Table II-82). Temporal fluctuations in biting activity were greatest at the ground level with a peak during 0700 hours and another peak from 1400 to 1600 hours. This species appeared to be most abundant at the Buenos Aires II (Table II-83) site but this was at least partially due to an unusually large collection of 264 specimens on April 1, 1971. The relatively low number per period, for most of the months in the seasonal distribution, reflects the inclusion of the night periods with their very small number of individuals. P. albipes did not seem to have a distinct pattern of seasonal distribution (Table II-84) that can be related to the local rainfall which tends to suggest that this species may have been developing at a considerable distance away from the Providencia region. However, it should be noted that the very high population level that occurred in early April could have been related to the abnormally high March rainfall.

A summary of the mosquitoes submitted for virus isolation is given in Table II-95.

Table II-83. Temporal distribution of Psorophora albipes biting activity at different forest sites.

Period beginning	07	08	09	10	11	12	13	14	15	16	17	18	Totals
Buenos Aires I													
No. Taken	7	15	4	6	1	5	9	16	16	13	8	4	106
No. Periods	27	36	39	39	39	36	39	39	39	36	39	42	759
No./Period	0.33	0.42	0.10	0.15	0.03	0.14	0.23	0.41	0.41	0.36	0.20	0.09	0.14
Buenos Aires II													
No. Taken	48	24	22	44	45	27	46	41	60	30			387
No. Periods	39	39	42	42	42	42	42	42	42	36			408
No./Period	1.23	0.62	0.52	1.05	1.07	0.64	1.10	0.98	1.43	0.83			0.95
Providencia													
No. Taken	6	9	10	6	8	10	4	5	6	0	15	2	88
No. Periods	45	48	48	48	48	48	45	45	45	39	33	30	819
No./Period	0.13	0.19	0.21	0.12	0.17	0.21	0.09	0.11	0.13	0	0.45	0.07	0.11
Tiroteos													
No. Taken	24	22	18	16	23	24	24	39	36	6	14	1	255
No. Periods	45	45	45	45	45	45	45	45	45	39	30	27	759
No./Period	0.53	0.49	0.40	0.36	0.51	0.53	0.53	0.87	0.80	0.15	0.47	0.04	0.34

Table II-84. Seasonal distribution of Psorophora albipes biting activity.

	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
No. Taken	26	4	20	386	44	62	122	40	16	17	46	53
No. Periods	228	261	261	258	285	282	321	159	162	171	171	186
No./Period	0.11	0.02	0.07	1.50	0.15	0.22	0.38	0.25	0.10	0.10	0.27	0.28

Table II-85. Culicidae submitted for virus isolation.

<u>Aedes fluviatilis</u>	25
<u>Aedes septemstriatus</u>	4
<u>Anopheles neivai</u>	274
<u>Anopheles squamifemur</u>	1
<u>Culex</u> sp. A	796
<u>Haemagogus capricorni falco</u>	1310
<u>Haemagogus clarki</u>	168
<u>Haemagogus</u> spp. ^{1/}	99
<u>Psorophora albipes</u>	705
<u>Psorophora cingulata</u>	1
<u>Sabethes belisarioi</u>	307
<u>Sabethes chloropterus</u>	411
<u>Sabethes tarsopus</u>	13
<u>Sabethes</u> sp. A	12
<u>Sabethes</u> sp. B	39
<u>Trichoprosopon digitatum</u>	21
<u>Trichoprosopon longipes</u>	13
<u>Trichoprosopon magnus</u>	223
<u>Wyeomyia</u> spp.	64
TOTAL CULICIDS	4486

¹ Predominately H. capricorni falco with a few H. lucifer

Acknowledgments

The authors are indebted to a large number of people, without whose help this study would not have been possible. Undoubtedly, some deserving special thanks have been unintentionally omitted. Dr. Roy D. Shenefelt has given valuable advice throughout the course of this study but was particularly helpful in the planning of the study and in determining its final direction. Ms. Jan S. Porter contributed an enormous amount of her time during the field studies and has continually given invaluable support. We gratefully acknowledge the help of Mr. Jairo Parra who constructed the study sites and supervised many of the catches. During the field studies, Norman E. Peterson gave us valuable assistance on many occasions. The very helpful technical assistance from Ms. Mary Gleason and Ms. Fany Bustamante is gratefully acknowledged. Mr. David G. Young, Dr. G.B. Fairchild, and Dr. W. W. Wirth have given invaluable help with the identifications of, respectively, the Phlebotominae, Tabanidae, and Culicoides. We are indebted to Drs. Robert R. Kowal and Peter Nemenyi for invaluable statistical advice and the writing of several computer programs. Mr. Arden R. Hardie has also given us valuable assistance with computer programs. We would like to thank the Univ. of Wisconsin Plant Ecology Laboratory for the use of their programs BCORD and STEREO, and thank Dr. Martin J. Lechowicz for help in their implementation. We are indebted to Dr. Edward W. Beals for allowing us to use a portion of his field data concerning the distribution of vegetation at the Buenos Aires study sites and for his advice during various stages of data analysis. The help and assistance of Dr. T.M. Yuill throughout this study is gratefully acknowledged. This study would not have been possible without the help received from Dr. Gene R. DeFoliart

in obtaining additional financial assistance. We also thank Dr. DeFoliart for his advice throughout this study. We extend our gratitude to Pato Consolidated Gold Mines, Ltd. for their hospitality and for allowing us to use their land as a study area.

The Veterinary Faculty, Universidad de Antioquia, provided valuable assistance with logistics and laboratory space. Individuals, including workers, technicians, secretaries, faculty members and the administrative staff are too numerous to acknowledge individually, but contributed substantially to the entomological studies.

STUDIES IN LOWLAND AREAS

Previous studies of hematophagous Diptera in the Providencia study area indicated that while mosquitoes species were numerous, relative numbers of Culicidae in primary and secondary forests as well as clearings were very low. Consequently, an area forty miles distant, which had experienced considerably greater ecological disturbance, was selected as a site for additional entomological studies. The Caucasias site proved to be an area of mosquito abundance. The objectives of the Caucasias study were to determine which species were most abundant in this agro-ecosystem and to ascertain differences between wet and dry seasons. Mosquitoes were collected and shipped to the virus laboratory in Medellin and were processed there for virus isolation.

The Caucasias area is low and hilly. Most of the region has been cleared and only small scattered forested areas remain. These forests range in size from 10 to 50 hectares and exist where further clearing would not be economical, as along streams or in low lying areas which are inundated throughout much of the year. A few upland forests remain on some of the larger cattle ranches and are preserved as a source of timber and fence posts.

Originally four haciendas were selected for study and collecting (Fig. II-32) began in December, 1971. Selection of these study areas was based on a preliminary survey. The greatest variation in habitats and species existed at Haciendas Barro, Buenos Aires, California, and Cuba.

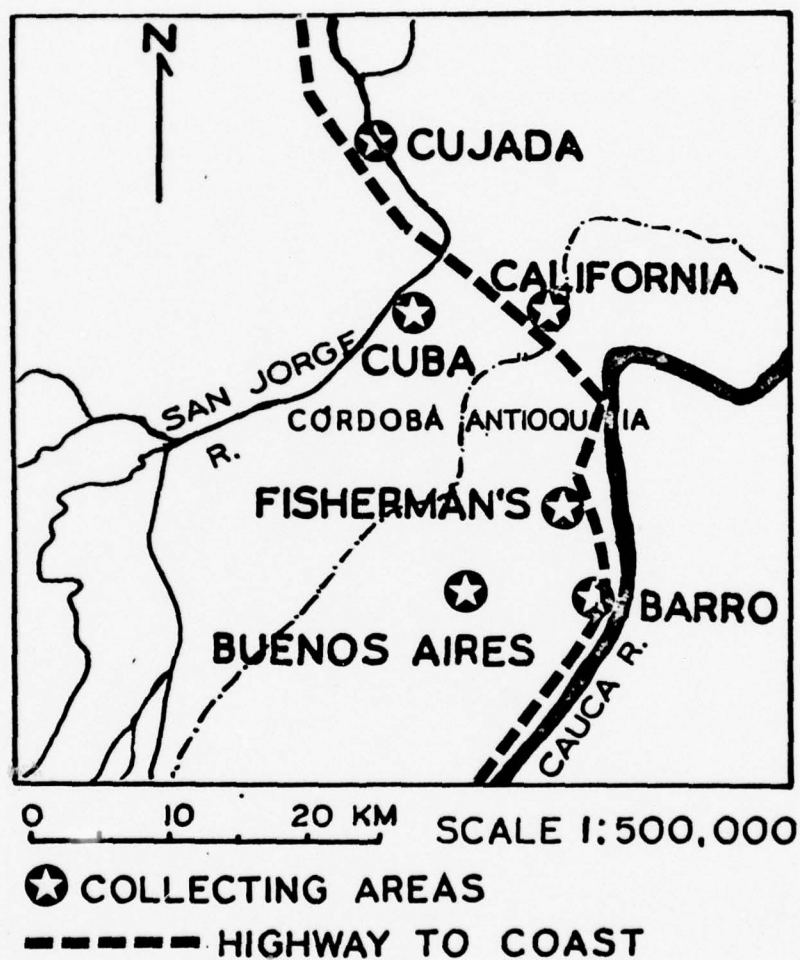


Figure II-32. Insect collecting sites in the Cauca, Antioquia, area.

Hacienda California, which also served as the field laboratory, was located 11.4 kilometers northwest of Caucaasia in the Department of Cordoba. This hacienda differed from the other three by not having any major rivers in the immediate area. It also differed in being classified as mainly high pasture. Although, several low lying areas were present, these were completely dry during the hot, dry season. There were several large artificial ponds which served as water sources, and were possible breeding places for Culex (Melanoconion spp.). These ponds experienced a significant reduction in the water volume during the 1972-1973 dry season (December through March). During this drought several small streams, which during the previous dry season contained water pools, were completely dry.

At California, initially two light trap and aspiration sites were selected. One site was located one hundred meters west of the ranch buildings. This site was located in a mango grove consisting of twelve trees. Although these trees provided some cover for resting mosquitoes, the area was heavily grazed and during the dry season little ground cover existed. Two small ponds lie about twenty-five meters north of the mango grove and could have provided breeding places for Culex, Psorophora and Aedes. The second site was located in the only wooded area on the hacienda. This wooded area was located on high ground with low areas to the west and south. The forest consisted of approximately twenty hectares. Some of the trees reached twenty meters in height. Light trap and aspirated collections were taken twenty meters into this forest. Aspirations were also taken along a road leading into the center of the area. Since no initial differences were noted in

the light trap collections obtained here from those in the wooded sites on the other haciendas, light trapping was discontinued here due to the difficulty in transporting traps with the onset of the rainy season.

Hacienda Cuba was also located in the Department of Cordoba. It was 11.2 kilometers by road from the field lab. Located along the Son Jorge River, the area was mainly low pasture with many ponds and inundated areas. During the dry season (December-March), one large area remained inundated. Initially only one site was selected for light and aspiration collections. This site was located in an orange, pineapple and mango grove twenty-five meters south of the worker's quarters. This grove was bounded by the San Jorge River 100m to the west, and a small pond 10m to the east. During December some of the depressions within this grove had standing water. Further examination of the area resulted in the addition of another sampling site in May. This site was located along the road leading into the hacienda. It was a low lying inundated area of brush (3-4 meters high) located in open pasture. Although the collections here were small, a species of Culex (Melanoconion) was present that was not collected at any of the other sites.

During June of 1972, one of the major collecting areas of hacienda Cuba was physically disturbed. The pineapple plants underneath the large mango trees near the river were removed as were several of the orange trees. At this time, construction of a new ranch house was begun at the former location of the worker's quarters. This construction continued through the end of the study in March, 1973.

Hacienda Barro (Department of Antioquia) was located 12 kilometers south of Caucasia on the Cauca River. This hacienda had more varied habitats

than any of the other ranches studied. Three sampling sites were selected. One site was located just north of the main ranch house (approximately 45 meters) next to a permanent pond of about 1/8 hectare. The Cauca River was about eighty meters to the east. This site had good ground cover of uncut grass and was shaded by several trees. There were also several pineapple plants, which may have provided breeding sites for Wyeomia spp. The second site was located approximately 3/4 kilometers south of the buildings. It was located along a wooded stream about one hundred and fifty meters from the Cauca River. Although most of the cover was under three meters in height, several large trees (15-20 meters) were present. To the east between the stream and the Cauca River was a broad flat expanse of low open pasture. Examination of this area revealed many small depressions and hoof prints which could have served as breeding areas for mosquitoes during the rainy season. The third and last site was located west of the buildings approximately six hundred meters west of the main highway. This location was just into the interior of a forty hectare stand of forest. A small stream was located fifty meters to the west of the sampling site. This stream, during the dry season, had water only in the areas where there had been large deep pools.

In addition to the light trap and aspiration collections, in 1972-73 stable traps were used at the edge of the large secondary forest at the hacienda. This trap was baited with a burro in the morning and the animal was removed the following morning. Insects which had entered the side baffles of the trap were aspirated from the inside and handled similarly to those collected by other methods.

Hacienda Buenos Aires was located on the Man River approximately 14 kilometers northwest of Guarumo. Entrance into this collecting area was restricted by the poor condition of the road during the rainy season. Two light sampling and three aspirator sites were maintained. One light trap and aspirator site was located 1.5 kilometers east of the buildings in a fifty (approximately) hectare patch of forest. This site was on high ground. Two ponds were located in open pasture approximately three hundred meters southeast of the sampling site. A deeply rutted tractor trail ran through the wooded area and, after a rain, served as a mosquito breeding place. Reaching this site after a rain presented some problems. It was possible to drive within three kilometers when the road was dry, but when wet, passage was on foot or horse back. A second light and aspirator site was located along a wooded stream in open pasture. Although many depressions and hoof prints were present, the rains were sufficient to maintain them as breeding sites. This second site was approximately 4.5 kilometers from the buildings and 9.5 kilometers from the entrance point at Guarumo. A third aspiration site was selected west of the river. Collections here were made only when the weather permitted entrance to the main ranch by truck. This site was located 2 kilometers north of the buildings in a forested area surrounded by low, wet pasture.

In addition to the collecting sites on the four ranches, two new sites were added in December, 1972. Light trapping was done beginning in October, 1972, at a site called the Fisherman's Hut. This site was located 5.2 kilometers south of Caucasia, west of the highway approximately 1/2 kilometer south of the Man River. The Cauca River lay approximately 1/2 kilometer

to the east. This area was marshy in the lowlands with brushy areas and scattered trees in the uplands. The area was susceptible to flooding during extremely high waters.

The second new sampling site was at Hacienda Cujada. Collecting was begun on the 12th of July, 1972. Cujada was located 12.5 kilometers northwest of Hacienda California. A collecting site was selected in the open approximately 3.4 kilometers east of the ranch buildings and 1 kilometer west of the main road. This site was located on the north corner of a lake of approximately 90 hectares. Open, brushy pasture lay to the north and west of the pond and brushy areas to south and east. A forested area lay approximately 200 meters to the south. Part of the brushy area was cleared and burned in December of 1972. A second collecting site was located 1/2 kilometer west of the lake, midway along the forested area. The forest was secondary with trees ranging between 4 and 10 meters in height, most being less than 6 meters. Although some undergrowth was present, the area had been grazed and relatively little ground cover remained.

Methods

A variety of collecting methods were used throughout the study in an attempt to avoid technique-induced bias. Collecting was done in distinct habitats including forested areas, brushy areas, open pasture, and open areas with little cover.

Insects were mainly captured by aspiration and with light traps. Insects attracted to, and usually alighting upon, the collectors were captured with a simple mouth aspirator, and then gently blown into cages made from pint or quart ice cream cartons. Standard CDC light traps were also used. These traps were powered by 6 volt automobile or motorcycle batteries. These traps were modified in that the cloth mesh bags into which the insects are normally blown and retained were replaced with modified quart ice cream cartons with small screened windows. Excelsior was placed into the cartons.

Burro-baited Magoon stable traps¹ were used for the last year of the study. Insects were aspirated from the inside of the trap and transported to the field laboratory in ice cream carton cages. A gasoline-powered D-Vac mechanical aspirator was also periodically used to sweep insects resting in low vegetation.

Problems were encountered in the transportation of insects from the collecting sites to the field lab at Hacienda California. Loss of insects due to dessication was the greatest in the transportation of light trap collections from Hacienda Buenos Aires. These losses occurred because of the amount of time needed in returning from the collecting sites. Under ideal conditions forty minutes was needed in traveling from the collecting sites to the field lab where identification and sorting into pools took place. The travel time required, high temperatures and movement over rough roads often

resulted in total loss. Similar problems were experienced in the transportation and holding of blood-engorged mosquitoes collected by aspiration. The problem of transportation of both the light trap and aspirated collections was eventually solved by placing them in a styrofoam cooler containing a small amount of ice. The aspirated collections were transferred to round gallon ice cream containers with moistened tissue paper in the bottom and screen tops as added precautions. The paper served as a source of water and humidity, further reducing the problem of dessication.

In the case of blood-engorged specimens, which had to be held for 24-36 hours before being sorted into pools, mortality was further reduced by placing another piece of moistened tissue paper on the surface of the container. This tissue once again served as a source of water which enabled the mosquitoes to maintain a water balance and reduced losses which had been encountered when the tissue paper in the bottom had dried up. The tissue paper had to be remoistened every eight hours.

In the field laboratory, insects were anesthetized with CO_2 or chloroform and sorted by species, day of capture and location. Individuals for which classification was not certain were saved for later identification. Pools of up to 100 mosquitoes, phlebotomines and simulids and up to five tabanids were frozen on dry ice, and shipped to the base laboratories for virus isolation attempts.

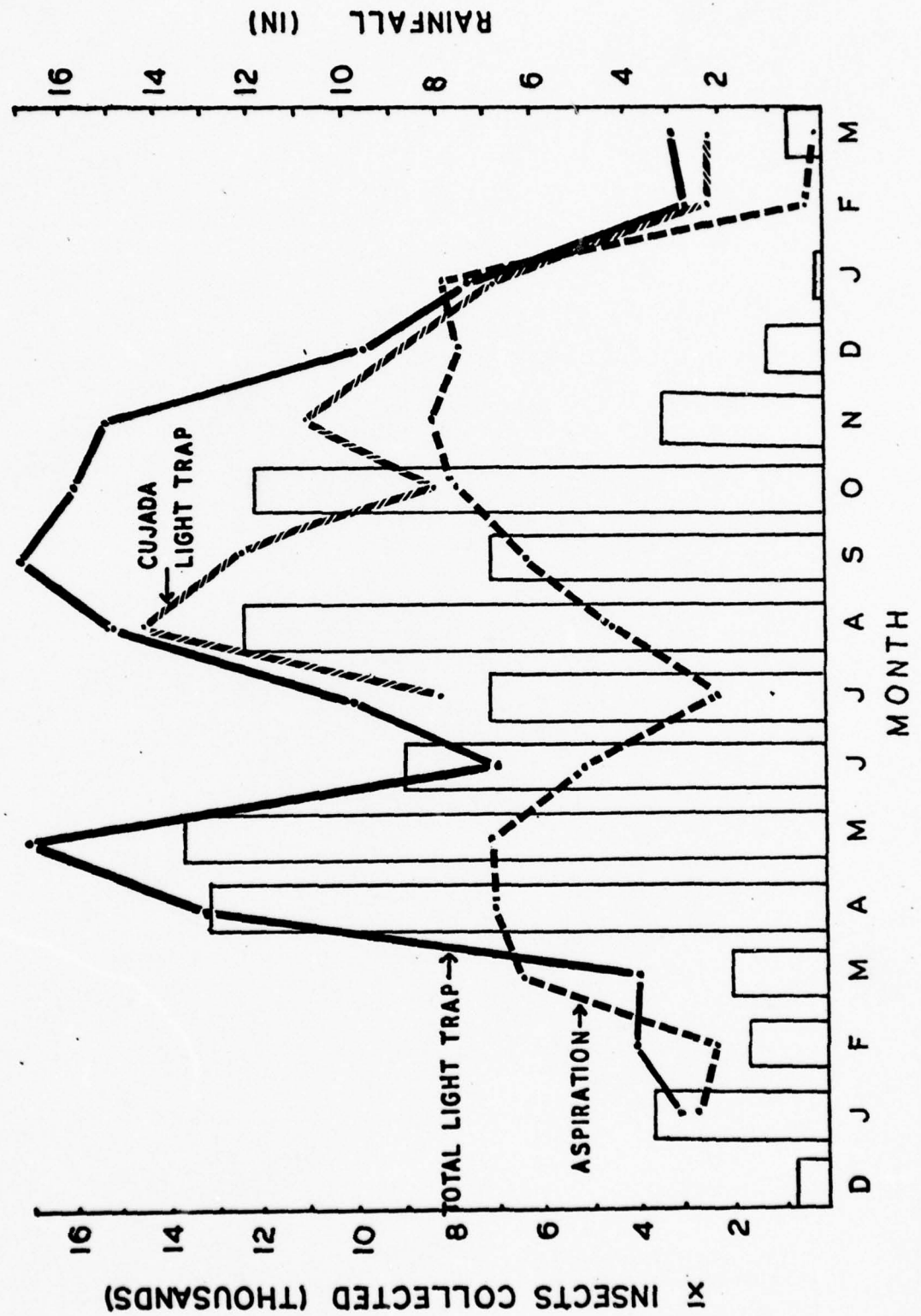
RESULTS

The Caucasia area proved to be very rich in mosquito fauna. In all, 51,683 mosquitos representing 34 species were collected. The actual number of species is expected to be higher since some of the species are so closely related as to be nearly indistinguishable. Ceratopogonids, phlebotomines and tabanids were also collected. The Caucasia area, however, was much more impoverished with respect to these later groups than was the Providencia area.

The number of hematophagous insects collected in the Caucasia area appeared to have been related to rainfall (Fig. II-25). Abundant rainfall occurred from March through October. Both light trap and aspiration catches of insects were high during this period, but declined to low values during the November-March dry season (Table II-86).

Some trends were observed throughout the current study. Some species showed distinct preferences, but absence or presence in any of these habitats was biased by the capture method used and the climatic conditions in the area as well as the habit of the species. Some species showed a distinct preference for forested habitats. Aedes scapularis, A. serratus, a light brown Culex species, a dark species of Culex (Melanoconion), Psorophora albipes, and P. ferox showed distinct preferences for the forest habitat. Aedeomyia squamipenna, a Culex with black spots and an undetermined Wyeomia species were principally found in the brushy areas. Anopheles triannulatus, Aedes crinifer, a tan species of Culex (Melanoconion), Mansonia nigricans, M. titillans, Psorophora cingulata, and P. confinnis were the species collected principally in the open areas.

Figure II-33. Light trap and aspiration collection of hematophagous insects (lines) vs rainfall (bars) in the Caucasus area.



Certain collecting methods were apparently much more effective with some species than were other techniques (Table II-87). Most of the Anopheles the majority of the Culex species, as well as most of the Mansonia and some of the Psorophora species were collected frequently in light traps but seldom in human biting collections. On the other hand, many Aedes, Psorophora albipes, P. ferox, and Wyeomia species were collected as they attempted to bite man. Most of the tabanids were captured in biting collections as well. The ceratopogonids and phlebotomines were exclusively collected in light traps. The relative frequency of appearance of various species in light trap and biting collections was evaluated in the three habitats Tables II-88 and II-89. There was great variation in the number of individuals per collection in the three habitats ranging from 0.01 individuals per collection to a high of 47.7 per collection for the dark species of Culex (Melanoconion). Ceratopogonids were infrequent at only 1.45 individuals per collection. The phlebotomines were somewhat more abundant, 7.96 individuals having been captured per collection only every 30-100 collections.

Twelve mosquito species and 3 tabanid species were collected in the burro-baited stable trap in the Barro forest (Table II-90). Of these, Psorophora albipes and Mansonia titillans comprised 47% and 29% of the catch. Interesting, both species have been implicated as vectors of Venezuelan equine encephalitis, a virus which appears to be enzootic in the Caucasia area (see Part I of this report).

There were some striking differences in forest collections done at the various sites (Tables II-91 and II-92). Barro had both the greatest number as well as the greatest variety of mosquitoes collected of any of the ranches

studied. Buenos Aires was a close second. Relatively few mosquitoes were collected at California in the forest, but this was greatly influenced by the termination of collecting in the forest during the rainy season, when travel became considerably more difficult. A relatively large number of mosquitoes was collected at Cujada despite the fact that the area was sampled a shorter time than were the others. This may have been due, in part, to the close proximity of the light trap to the lake, a good mosquito breeding area. Cujada was a particularly good place for collection of Mansonia spp. Biting collections in the forest paralleled the light trap collections, with somewhat more mosquitoes having been collected at Barro than in the other three areas. Buenos Aires was nearly equal to Barro, however, with California and Cujada being considerably less. Only about half the number of insects was taken by biting collection as was taken in light traps. It should be remembered, however, that biting collections were only done over a short period of time (45-60 minutes) at midday and in late afternoon or early evening, whereas light trap collections ran for a period of 12 to 13 hours.

The Barro collecting site was also rewarding for mosquito collections in brushy areas (Tables II-93&94). There were over four times the number of biting Diptera collected there than in the other two areas together. The Barro area was also richer in phlebotomines and in tabanids. The biting collections in the brushy areas also paralleled those of the light traps in the same areas in terms of relative successfulness by site. With the exception of Cuba, nearly 10 times more insects were collected by light trap than were collected by aspiration, suggesting that the bulk of the mosquitoes coming into the brushy areas were active later at night.

The open grassy areas of five different sites were collected during the present report period (Tables II-95 and II-96). The Cujada area had the greatest abundance of open area mosquitoes, having over twice the number of mosquitoes collected than in all other areas together. There were 273 biting insects per collection at Cujada as opposed to 47 at the Fisherman's Hut, 32 in Cuba, 24 in Barro and only 17 in California. More ceratopogonids were also collected in Cujada than in the other areas. Phlebotomines were relatively scarce in the open as were tabanids. Interestingly, this same parallel of greatest light trap success was observed in open areas as well. Our light traps were almost twice as successful as were aspiration collections. One noteworthy exception was Barro, where nearly twice the number of insects were collected by aspiration than by light trap.

Another striking difference was the relative numbers of individuals per collection by site. In the biting collection, greatest success was experienced at Cuba, largely due to the large number of Aedes crinifer collected there in contrast to the light trap collections. Relatively few individuals were collected by biting collection at Cujada.

Work on the taxonomy of hematophagous Diptera from Caucasia continues in the home laboratory. The phlebotomines (Table II-102) and tabanids (Table II-103) have recently been classified. The Culex species of the area present particularly difficult taxonomic problems, especially in the absence of good collections of larvae and of males. The tentative identifications are given in Table II-104. Interestingly, six species of Culex (Melanonoconion) new to Colombia were collected. This subgenus is important as the principal vector of sylvan Venezuelan equine encephalitis virus in various parts of the Americas.

TABLE II-86 Monthly light trap (L), aspiration (A) and total (Σ) collection of the 10 most common Culicidae species in the Causasia area, February, 1972-March, 1973.

Month	February			March			April			May		
Collection Method	L	A	Σ	L	A	Σ	L	A	Σ	L	A	Σ
Number of Collections	21	15	36	13	11	24	17	19	36	10	10	20
SPECIES:												
Anopheles (Nyssorhynchus) triannulatus	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (0.11)	0 (0)	2 (0.05)	30 (3.0)	0 (0)	30 (1.5)
Aedeomyia squamipennis	111 (5.3)	0 (0)	111 (5.3)	7 (0.53)	0 (0)	7 (0.53)	21 (1.2)	0 (0)	21 (0.58)	52 (5.2)	0 (0)	52 (2.6)
Aedes crinifer	2 (0.09)	59 (3.9)	61 (1.7)	1 (0.07)	33 (3.0)	34 (1.4)	20 (1.2)	124 (6.5)	144 (4.0)	19 (1.9)	82 (8.2)	101 (5.1)
Aedes scapularis	29 (1.4)	186 (12.4)	215 (6.0)	18 (1.4)	553 (50.3)	571 (23.8)	29 (1.7)	717 (37.7)	746 (20.7)	13 (1.3)	97 (9.7)	110 (5.5)
Aedes serratus	2 (0.09)	29 (1.9)	31 (0.86)	0 (0)	37 (3.4)	37 (1.5)	12 (0.7)	88 (4.6)	100 (2.8)	4 (0.4)	51 (5.1)	55 (2.8)
Culex sp. Lt. brown	330 (15.7)	0 (0)	330 (15.7)	178 (13.7)	0 (0)	178 (7.4)	771 (45.4)	1 (0.05)	772 (21.4)	427 (42.7)	1 (0.1)	428 (21.9)
C. (Melanoconion) sp. dark	161 (7.7)	0 (0)	161 (7.7)	125 (9.6)	0 (0)	125 (5.2)	856 (50.4)	0 (0)	856 (23.8)	537 (53.7)	0 (0)	537 (26.9)
Mansonia nigricans	62 (3.0)	0 (0)	62 (3.0)	23 (1.8)	0 (0)	23 (0.95)	2 (0.11)	0 (0)	2 (0.05)	74 (7.4)	6 (0.6)	80 (4.0)
Mansonia titillans	12 (0.57)	4 (0.26)	16 (0.44)	26 (2.0)	10 (0.90)	36 (1.5)	16 (0.94)	1 (0.05)	17 (0.47)	18 (1.8)	3 (0.3)	21 (1.1)
Psorophora albipes	9 (0.42)	38 (2.53)	47 (1.3)	5 (0.38)	64 (5.8)	69 (2.9)	0 (0)	2 (0.10)	2 (0.05)	28 (2.8)	402 (40.1)	430 (21.5)

TABLE II-86. (Continued)

Month	June			July			August			September		
Collection Method	L	A	Σ	L	A	Σ	L	A	Σ	L	A	Σ
Number of Collections	10	11	21	20	8	28	23	24	47	37	33	70
SPECIES:												
<i>Anopheles</i> (<i>Nyssorhynchus</i>) <i>triannulatus</i>	2 (0.2)	1 (0.1)	3 (0.14)	162 (8.1)	1 (0.12)	163 (5.8)	354 (15.4)	1 (0.04)	355 (7.6)	1798 (48.6)	5 (0.15)	1803 (25.8)
<i>Aedeomyia</i> <i>squamipennis</i>	0 (0)	0 (0)	0 (0)	218 (1.1)	0 (0)	218 (7.8)	629 (27.3)	0 (0)	629 (13.4)	417 (11.3)	0 (0)	417 (6.0)
<i>Aedes</i> <i>crinifer</i>	0 (0)	105 (9.5)	105 (5.0)	2 (0.1)	107 (13.4)	109 (3.9)	22 (0.95)	389 (16.2)	411 (8.7)	17 (0.45)	816 (24.7)	833 (11.9)
<i>Aedes</i> <i>scapularis</i>	0 (0)	22 (2.0)	22 (1.0)	0 (0)	0 (0)	0 (0)	0 (0)	5 (0.20)	5 (0.10)	0 (0)	3 (0.09)	3 (0.04)
<i>Aedes</i> <i>serratus</i>	0 (0)	20 (1.8)	20 (0.95)	1 (0.05)	15 (1.9)	16 (0.57)	0 (0)	25 (1.0)	25 (0.53)	4 (0.10)	50 (1.5)	54 (0.77)
<i>Culex</i> sp. Lt. brown	40 (4.0)	0 (0)	40 (1.9)	226 (11.3)	0 (0)	226 (8.1)	488 (21.2)	4 (0.16)	492 (10.5)	271 (7.3)	0 (0)	271 (3.9)
<i>C. (Melanoconion)</i> sp. dark	166 (16.6)	0 (0)	166 (7.9)	561 (28.1)	0 (0)	561 (20.0)	1245 (54.1)	0 (0)	1245 (26.5)	2064 (55.8)	0 (0)	2064 (29.5)
<i>Mansonina</i> <i>nigricans</i>	21 (2.1)	6 (0.54)	27 (1.3)	44 (2.2)	2 (0.25)	46 (1.6)	197 (8.6)	34 (1.4)	231 (4.9)	656 (17.7)	94 (2.8)	750 (10.7)
<i>Mansonina</i> <i>titillans</i>	5 (0.5)	28 (2.5)	33 (1.6)	321 (16.1)	6 (0.75)	327 (11.7)	245 (10.7)	73 (3.0)	318 (6.8)	410 (11.1)	77 (2.3)	487 (6.9)
<i>Psorophora</i> <i>albipes</i>	12 (1.2)	264 (24.0)	276 (13.1)	2 (0.1)	32 (4.0)	34 (1.2)	44 (1.9)	441 (18.4)	485 (10.3)	26 (0.7)	676 (20.5)	702 (10.0)

TABLE II- 86 (continued)

Month	October			November			December			January		
	L	A	Σ	L	A	Σ	L	A	Σ	L	A	Σ
Collection Method												
Number of Collections	31	22	53	28	26	54	37	27	64	44	25	69
SPECIES:												
<i>Anopheles</i> (<i>Nyssorhynchus</i>) <i>triannulatus</i>	931 (30.0)	2 (0.09)	933 (17.6)	794 (28.4)	2 (0.07)	796 (14.7)	188 (5.1)	1 (0.03)	189 (3.0)	117 (2.7)	1 (0.04)	118 (1.7)
<i>Aedeomyia</i> <i>squamipennis</i>	418 (13.5)	0 (0)	418 (7.9)	437 (15.6)	0 (0)	437 (8.1)	318 (8.6)	0 (0)	318 (5.0)	207 (4.7)	0 (0)	207 (3.0)
<i>Aedes</i> <i>crinifer</i>	93 (3.0)	677 (30.8)	770 (14.5)	85 (3.0)	911 (35.0)	996 (18.4)	35 (0.94)	920 (34.1)	955 (14.9)	9 (0.2)	593 (23.7)	602 (8.7)
<i>Aedes</i> <i>scapularis</i>	0 (0)	2 (0.09)	2 (0.03)	4 (0.14)	84 (3.2)	88 (1.6)	4 (0.1)	148 (5.5)	152 (2.4)	5 (0.11)	236 (9.4)	241 (3.5)
<i>Aedes</i> <i>serratus</i>	22 (0.70)	55 (2.5)	77 (1.5)	15 (0.53)	151 (5.8)	166 (3.1)	23 (0.62)	256 (9.5)	279 (4.4)	3 (0.06)	252 (10.1)	255 (3.7)
<i>Culex</i> sp. Lt. brown	581 (18.7)	0 (0)	581 (11.0)	223 (8.0)	0 (0)	223 (4.1)	159 (4.3)	3 (0.11)	162 (2.5)	123 (2.8)	4 (0.16)	127 (1.8)
<i>C. (Melanoconion)</i> sp. dark	1208 (39.0)	0 (0)	1208 (13.0)	1080 (38.6)	0 (0)	1080 (20.0)	107 (2.9)	0 (0)	107 (1.7)	818 (18.6)	2 (0.08)	820 (11.9)
<i>Mansonella</i> <i>nigricans</i>	566 (18.3)	64 (2.9)	630 (11.9)	450 (16.1)	44 (1.7)	494 (9.1)	471 (12.7)	165 (6.1)	636 (9.9)	640 (14.5)	63 (2.5)	703 (10.2)
<i>Mansonella</i> <i>citrillians</i>	545 (17.6)	20 (0.9)	565 (8.1)	406 (14.5)	30 (1.2)	436 (8.1)	437 (11.8)	36 (1.3)	473 (7.4)	267 (6.1)	48 (1.9)	315 (4.6)
<i>Psorophora</i> <i>albipes</i>	107 (3.5)	730 (33.2)	837 (12.0)	59 (2.1)	796 (30.6)	855 (15.8)	34 (0.91)	490 (18.1)	524 (8.2)	12 (0.27)	476 (19.0)	488 (7.1)

TABLE II-86 (continued)

Month	February			March		
Collection Method	L	A	Σ	L	A	Σ
Number of Collections	33	25	58	33	25	58
SPECIES:						
Anopheles (Nyssorhynchus) triannulatus	60 (1.8)	0 (0)	60 (1.0)	198 (6.0)	2 (0.08)	200 (3.4)
Aedeomyia squamipennis	33 (1.0)	0 (0)	33 (0.56)	52 (1.6)	0 (0)	52 (0.89)
Aedes crinifer	0 (0)	1 (0.04)	1 (0.01)	0 (0)	0 (0)	0 (0)
Aedes scapularis	0 (0)	15 (0.60)	15 (0.25)	0 (0)	2 (0.08)	2 (0.03)
Aedes serratus	0 (0)	19 (0.76)	19 (0.32)	0 (0)	0 (0)	0 (0)
Culex sp. Lt. brown	82 (2.5)	4 (0.16)	86 (1.5)	209 (6.3)	0 (0)	209 (3.6)
C. (Melanoconion) sp. dark	130 (3.9)	4 (0.16)	134 (2.3)	152 (4.6)	0 (0)	152 (2.6)
Mansonella nigricans	166 (5.0)	7 (0.28)	173 (3.0)	137 (4.2)	0 (0)	137 (2.4)
Mansonella titillans	67 (2.0)	11 (0.4)	78 (1.3)	80 (2.4)	7 (0.28)	87 (1.5)
Psorophora albipes	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)

Table II-87. Hematophagous Diptera collected in light traps and while alighting on or biting man in three habitat types in Caucasia

Family/species	Forest		Brush		Open		Grand Totals	
	Light	Biting Total	Light	Biting Total	Light	Biting Total	Light	Biting Total
Ceratopogonidae	102	102	168	168	256	256	526	526
Culicidae								
Anophelinae								
A. (Anopheles) neomaculipalpus	10	10	25	25	26	26	61	61
A. (Anopheles) pseudopunctipennis		1	2	2	3	3	5	6
A. (Anopheles) punctimacula			11	11	32	32	43	43
A. (Lophodomyia) squamifemur	4	4	1	1			5	5
A. (Anopheles) sp.	2	2					2	2
A. (Nyssorhynchus) albitarsis	11	12	10	10	2	12	31	34
A. (Nyssorhynchus) albitarsis	6	6	16	16			22	22
A. (Nyssorhynchus) darlingi	1	1	3	3	1	17	20	21
A. (Nyssorhynchus) oswaldoi	29	29	8	8	2	20	55	58
A. (Nyssorhynchus) triannulatus	85	96	246	248	4305	4308	4636	4652
A. (Nyssorhynchus) sp.	8	8	13	13	17	17	38	38
Culicinae								
Aedeomyia squamipenna	123	123	2075	2075	734	734	2932	2932
A. (Ochlerotatus) crinifer	23	1100	57	643	225	3073	305	4816
A. (Ochlerotatus) scapularis	66	1262	24	271	17	562	107	2095
A. (Ochlerotatus) serratus	58	887	16	64	12	102	86	1053
A. (Ochlerotatus) sp.	52	475	48	27	189	543	289	1045
Culex sp. lt. br.	2387	9	1460	1460	325	6	4172	15
Culex sp.	60	60	30	30	50	50	140	140
C. (Melanoconion) sp. br.	94	94	159	159	50	50	303	303
C. (Melanoconion) sp. dark	4809	6	5153	5153	403	403	10365	6
C. (Melanoconion) sp. black	109	109	147	147	28	28	284	284
C. (Melanoconion) sp. gr. pleura	21	21	36	36	36	36	93	93
C. (Melanoconion) sp. blk. spots	76	77	193	193	5	5	274	1
C. (Melanoconion) sp. white tarsi	28	28	9	9	4	4	41	41
C. (Melanoconion) sp. gold spot	66	67	49	49	67	67	182	1
C. (Melanoconion) tan	8	8	59	60	330	331	397	2
C. (Melanoconion) sp.	9	9	4	4	12	12	25	25

Table II-87 (cont)

Family/species	Forest			Brush			Open			Grand Totals		
	Light	Biting	Total	Light	Biting	Total	Light	Biting	Total	Light	Biting	Total
<i>Mansonia</i> (<i>Mansonia</i>) <i>humeralis</i>	12	1	13	70		70	411	4	415	493	5	502
<i>M.</i> (<i>Rhynchoaenia</i>) <i>juxtamansonia</i>	8		8	46		46				54		54
<i>M.</i> (<i>Rhynchoaenia</i>) <i>nigricans</i>	1133	469	1602	996	10	1006	1409	19	1428	3538	498	4036
<i>M.</i> (<i>Mansonia</i>) <i>pseudotitillans</i>	12		12	3		3				15		15
<i>M.</i> (<i>Mansonia</i>) <i>titillans</i>	337	239	576	1120	80	1200	1423	47	1470	2880	366	3246
<i>M.</i> sp.	10	5	15	20	1	21	20		20	50	6	56
<i>Psorophora</i> (<i>Janthinosoma</i>) <i>albipes</i>	132	2330	2462	120	1538	1658	107	855	962	359	4723	4120
<i>P.</i> (<i>Grabhamia</i>) <i>cingulata</i>	21	38	59	60	26	86	186	32	218	267	96	363
<i>P.</i> (<i>Grabhamia</i>) <i>confinnis</i>	2		2	28	4	32	168		168	198	4	202
<i>P.</i> (<i>Janthinosoma</i>) <i>ferox</i>	4	400	404	7	69	76	1	33	34	12	502	514
<i>Limatus asulleptus</i>					1	1					1	1
<i>Trichoprosopon digitatum</i>		6	6		13	13					19	19
<i>T. longipes</i>		4	4		11	11					15	15
<i>Wyeomia</i> sp.		39	39	11	51	62		22	22	11	112	123
Psychodidae												
Phlebotominae	1301		1301	1424		1424	154		154	2879		2879
Tabanidae												
<i>Chrysops varians</i>		8	8		7	7					15	15
<i>C. varigatus</i>		6	6	2	6	8		2	2	2	14	16
<i>Lepiselaga crassipes</i>		5	5	2	1	3	1		1	3	6	9
<i>Tabanus</i> sp. 1		11	11		5	5					16	16
<i>T.</i> sp. 2	3	2	5	8	2	10	9		9	20	4	24
<i>T.</i> sp. 3		2	2	1		1	1		1	2	2	4
TOTALS	11222	7319	18541	13940	2833	16773	11060	5309	16369	36222	15461	51683

Table II-88. Hematophagous Diptera collected by light traps in three habitat types in Caucasia, November 1971 through March 1972

Family/species	Forest Σ (No./Coll.)	Brush Σ (No./Coll.)	Open Σ (No./Coll.)	Total Σ (No./Coll.)
Ceratopogonidae				
	102(0.94)	168(1.56)	256(1.77)	526(1.45)
Culicidae				
Anophelinae				
Anopheles (Anopheles) neomaculipalpus	10(0.09)			61(0.17)
A. (Anopheles) pseudopunctipennis		15(0.23)	26(0.18)	5(0.01)
A. (Anopheles) punctimacula		2(0.02)	3(0.02)	43(0.12)
A. (Lophodomyia) squamifemur	4(0.04)	11(0.10)	32(0.22)	5(0.01)
A. (Anopheles) sp.	2(0.02)	1(0.01)		2(0.01)
A. (Nyssorhynchus) albitarsis	5(0.05)	4(0.04)	13(0.09)	22(0.06)
A. (Nyssorhynchus) albimanus	6(0.06)	16(0.15)		22(0.06)
A. (Nyssorhynchus) darlingi	1(0.01)	3(0.03)	16(0.11)	20(0.06)
A. (Nyssorhynchus) oswaldoi	29(0.27)	10(0.09)	18(0.12)	57(0.16)
A. (Nyssorhynchus) triannulatus	85(0.78)	246(2.28)	4305(29.69)	4636(12.81)
A. (Nyssorhynchus) sp.	8(0.07)	13(0.12)	17(0.12)	38(0.10)
Culicinae				
Aedeomyia squamipenna	66(0.61)	2118(19.61)	837(5.77)	3032(8.38)
A. (Ochlerotatus) crinifer	23(0.21)	57(0.53)	225(1.55)	305(0.84)
A. (Ochlerotatus) scupularis	66(0.61)	24(0.22)	17(0.12)	107(0.30)
A. (Ochlerotatus) serratus	58(0.53)	16(0.15)	12(0.08)	86(0.24)
A. (Ochlerotatus) sp.	52(0.48)	48(0.44)	189(1.30)	289(0.80)
Culex sp. T. br.	2387(21.90)	1460(13.52)	325(2.24)	4172(11.52)
C. sp.	60(0.55)	30(0.28)	50(0.34)	140(0.39)
C. (Melanoconion) sp. br.	94(0.86)	159(1.47)	50(0.34)	303(0.84)
C. (Melanoconion) sp. dark	4809(44.12)	5153(47.71)	403(2.78)	10365(28.63)
C. (Melanoconion) sp. black	109(1.00)	147(1.36)	28(0.19)	284(0.78)
C. (Melanoconion) sp. green pleura	26(0.24)	36(0.33)	36(0.25)	98(0.27)
C. (Melanoconion) black with spots	76(0.70)	193(1.79)	5(0.03)	274(0.76)
C. (Melanoconion) sp. white tarsi	28(0.26)	9(0.08)	4(0.03)	41(0.11)
C. (Melanoconion) sp. gold spot	66(0.61)	49(0.45)	69(0.48)	184(0.51)
C. (Melanoconion) sp. tan	8(0.07)	59(0.55)	328(2.26)	395(1.09)
C. (Melanoconion) sp.	9(0.08)	4(0.04)	12(0.08)	25(0.07)

Table II-88. (cont.)

<u>Family/species</u>	Forest Σ(No./Coll.)	Brush Σ(No./Coll.)	Open Σ(No./Coll.)	Total Σ(No./Coll.)
<u>Mansonia (Mansonia) humeralis</u>	12(0.11)	70(0.65)	411(2.83)	493(1.36)
<u>M. (Rhynchoetaenia) juxtamansonia</u>	8(0.07)	46(0.43)		54(0.15)
<u>M. (Rhynchoetaenia) nigricans</u>	1133(10.39)	995(9.21)	1409(9.72)	3537(9.77)
<u>M. (Mansonia) pseudotitillans</u>	12(0.11)	3(0.03)		15(0.04)
<u>M. (Mansonia) titillans</u>	337(3.09)	1120(10.37)	1423(9.81)	2880(7.96)
<u>M. sp.</u>	10(0.09)	20(0.19)	20(0.14)	50(0.14)
<u>Psorophora (Janthinosoma) albipes</u>	132(1.21)	120(1.11)	107(0.74)	359(0.99)
<u>P. (Grabhamia) cingulata</u>	21(0.19)	60(0.56)	186(1.28)	267(0.74)
<u>P. (Grabhamia) confinnis</u>	2(0.02)	28(0.26)	168(1.16)	198(0.55)
<u>P. (Janthinosoma) ferox</u>	4(0.04)	7(0.06)	1(0.01)	12(0.03)
<u>Limatus asulleptus</u>				
<u>Trichoprosopon digitatum</u>				
<u>T. longipes</u>		11(0.10)		11(0.03)
<u>Wyeomia sp.</u>				
Psychodidae				
Phlebotominae				
	1301(11.94)	1424(13.19)	155(1.07)	2880(7.96)
Tabanidae				
<u>Chrysops varians</u>		2(0.02)		2(0.01)
<u>C. varigatus</u>		2(0.02)	1(0.01)	3(0.01)
<u>Lepiselaga crassipes</u>		8(0.07)	9(0.06)	20(0.06)
<u>Tabanus sp. 1</u>	3(0.03)	1(0.01)	1(0.01)	2(0.01)
<u>T. sp. 3</u>				
TOTAL	11,175(102.52)	13978(129.43)	11167(77.01)	36,320(100.33)

Table II-89. Hematophagous Diptera collected while alighting on or biting man in three habitat types in Caucasasia, November 1971 through March, 1972

Family/species	Forest			Brush			Open			Total		
	Σ (No./Coll.)	Σ (No./Coll.)	Σ (No./Coll.)	Σ (No./Coll.)	Σ (No./Coll.)	Σ (No./Coll.)	Σ (No./Coll.)	Σ (No./Coll.)	Σ (No./Coll.)	Σ (No./Coll.)	Σ (No./Coll.)	Σ (No./Coll.)
Culicidae												
Anophelinae												
A. (Anopheles) pseudopunctipennis	1 (0.01)										1 (4.01)	
A. (Nyssorhynchus) albitarsis	1 (0.01)							2 (0.02)			3 (0.01)	
A. (Nyssorhynchus) darlingi								1 (0.01)			1 (4.01)	
A. (Nyssorhynchus) oswaldoi								2 (0.02)			2 (0.01)	
A. (Nyssorhynchus) triannulatus	11 (0.10)					2 (0.03)		3 (0.03)			16 (0.06)	
Culicinae												
A. (Ochlerotatus) crinifer	1100 (10.48)			643 (8.04)			3073 (30.73)				4816 (16.90)	
A. (Ochlerotatus) scapularis	1268 (12.08)			271 (3.39)			556 (5.56)				2095 (7.35)	
A. (Ochlerotatus) serratus	887 (8.45)			64 (0.80)			102 (1.02)				1053 (3.69)	
A. (Ochlerotatus) sp.	475 (4.52)			27 (0.34)			543 (5.43)				1045 (3.67)	
Culex sp. lt. br.	9 (0.09)						6 (0.06)				15 (0.05)	
C. (Melanoconion) sp. dark	6 (0.06)										6 (0.02)	
C. (Melanoconion) sp. black with spots	1 (0.01)										1 (<.01)	
C. (Melanoconion) sp. golden spot	1 (0.01)										1 (<.01)	
C. (Melanoconion) sp. tan				1 (0.01)			1 (0.01)				2 (0.01)	
Mansonia (Mansonia) humeralis								4 (0.04)			5 (0.02)	
M. (Rhynchotaenia) nigricans	1 (0.01)							19 (0.19)			498 (1.75)	
M. (Mansonia) titillans	469 (4.47)			10 (0.13)			47 (0.47)				366 (1.28)	
M. sp.	239 (2.28)			80 (1.00)							6 (0.02)	
Psorophora (Janthinosoma) albipes	5 (0.05)			1 (0.01)							4723 (16.57)	
P. (Grabhamia) cingulata	2330 (22.19)			1538 (19.23)			855 (8.55)				96 (0.34)	
P. (Grabhamia) confinnis	38 (0.36)			26 (0.33)			32 (0.32)				4 (0.01)	
P. (Janthinosoma) ferox	400 (3.81)			69 (0.86)			33 (0.33)				502 (1.76)	
Limatus asulleptus												
Trichoprosopon digitatum				1 (0.01)							1 (<.01)	
T. longipes	6 (0.06)			13 (0.16)							19 (0.07)	
Wyeomia sp.	4 (0.04)			11 (0.14)							15 (0.05)	
	39 (0.37)			51 (0.64)			22 (0.22)				112 (0.39)	
Tabanidae												
Chrysops varians	8 (0.08)			7 (0.09)							15 (0.05)	
C. varigatus	6 (0.06)			6 (0.08)			2 (0.02)				14 (0.05)	
Lepiselaga crassipes	5 (0.05)			1 (0.01)							6 (0.02)	
Tabanus sp. 1	11 (0.10)			5 (0.06)							16 (0.06)	
T. sp. 2	2 (0.02)			2 (0.03)							4 (0.01)	
T. sp. 3	2 (0.02)										2 (0.01)	
TOTAL	7325 (69.76)			28.33 (35.41)			5303 (53.03)				15,461 (54.25)	

Table II-90. Burro-baited stable trap collections at forest sites, Hacienda Burro, Sept. 1972-March, 1973

Family species	Trap Location	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Total
Culicidae									
Anophelinae									
Anopheles oswaldoi	Interior						1	7	8
	Edge						1		1
	Total						2	7	9
Culicinae									
Aedes crinifer	Interior		2	1	4		3		10
	Edge			1	3				4
	Total		2	2	7		3		14
A. fulvus	Interior		1	1					2
	Edge								
	Total		1	1					2
A. scapularis	Interior			2		2			4
	Edge								
	Total			2		2			4
A. serratus	Interior	2	1	7	2	3			15
	Edge			2	1				3
	Total	2	1	9	3	3			18
Culex (Melanoconion) sp. dark	Interior		2	3					5
	Edge								
	Total		2	3					5
Mansonia nigricans	Interior	1			1				2
	Edge					1			1
	Total	1			1	1			3

Family species	Trap Location	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Total
<i>M. titillans</i>	Interior	9	3	6	1	5		1	25
	Edge		36	7	3	18	9	1	74
	Total	9	39	13	4	23	9	2	99
<i>Psorophora albipes</i>	Interior		22	85	7	2	1		117
	Edge		21	19	4	1			45
	Total		43	104	11	3	1		162
<i>P. cingulata</i>	Interior				1				1
	Edge								
	Total				1				1
<i>P. ferox</i>	Interior		7	7					14
	Edge		3						3
	Total		10	7					17
<i>Trichoprosopon digitatum</i>	Interior		1	2					3
	Edge								
	Total		1	2					3
<i>Wyeomyia</i> sp.	Interior		1						1
	Edge								
	Total		1						1
Tabanidae <i>Chrysops varians</i>	Interior				1				1
	Edge								
	Total				1				1
<i>Lepiselaga crassipes</i>	Interior					1			1
	Edge								
	Total					1			1
<i>Tabanus</i> sp 3	Interior		1						1
	Edge		1						1
	Total		2						2
TOTAL	Interior	13	40	114	17	13	5	8	210
	Edge	1	60	29	11	20	10	1	142
	Total	14	100	143	28	33	15	9	342

Table II-91

Hematophagous Diptera collected in light traps placed

in forested areas on four ranches

Family/species	Barro Σ(No./Coll.)	Buenos Aires Σ(No./Coll.)	California Σ(No./Coll.)	Cujada Σ(No./Coll.)
Ceratopogonidae				
102(2.91)				
Culicidae				
Anophelinae				
Anopheles (Anopheles) neomaculipalpus				10(0.42)
A. (Anopheles) pseudopunctipennis				
A. (Anopheles) punctimacula				
A. (Lophodomyia) squamifemur	4(0.10)		2(0.25)	
A. (Anopheles) sp.				
A. (Nyssorhynchus) albitarsis	1(0.02)			4(0.17)
A. (Nyssorhynchus) albimanus		2(0.06)		4(0.17)
A. (Nyssorhynchus) darlingi	1(0.02)			
A. (Nyssorhynchus) oswaldoi	10(0.24)	13(0.37)		6(0.25)
A. (Nyssorhynchus) triannulatus	4(0.10)	12(0.34)		69(2.88)
A. (Nyssorhynchus) sp.	5(0.12)		3(0.38)	
Culicinae				
Aedeomyia squamipennis	48(1.14)	17(0.49)		12(0.50)
A. (Ochlerotatus) crinifer	15(0.36)	5(0.14)		3(0.13)
A. (Ochlerotatus) scupularis	1(0.02)	50(1.43)	10(1.25)	5(0.21)
A. (Ochlerotatus) serratus	18(0.43)	3(0.09)		37(1.54)
A. (Ochlerotatus) sp.	31(0.74)	6(0.17)		15(0.63)
Culex sp. T. br.	1149(27.36)	1124(32.11)	78(9.75)	36(1.50)
C. sp.	1(0.02)	59(1.69)		
C. (Melanoconion) sp. br.	31(0.74)	63(1.80)		
C. (Melanoconion) sp. dark	2484(59.14)	1897(54.20)	46(5.75)	382(15.92)
C. (Melanoconion) sp. black	22(0.52)	82(2.34)	5(0.63)	
C. (Melanoconion) sp. green pleura	16(0.38)			10(0.42)
C. (Melanoconion) black with spots	76(1.81)			
C. (Melanoconion) sp. white tarsi	24(0.57)	2(0.06)		2(0.08)
C. (Melanoconion) sp. gold spot	18(0.43)	11(0.31)		37(1.54)
C. (Melanoconion) sp. tan	2(0.05)			6(0.25)
C. (Melanoconion) sp.	9(0.21)			

Table II-91 (cont)

Family/species	Barro Σ(No./Coll.)	Buenos Aires Σ(No./Coll.)	California Σ(No./Coll.)	Cujada Σ(No./Coll.)
<i>Mansonina</i> (<i>Mansonina</i>) <i>humeralis</i>	6(0.14)	4(0.11)		2(0.08)
<i>M.</i> (<i>Rhynchotaenia</i>) <i>juxtamansonina</i>	4(0.10)	4(0.11)		
<i>M.</i> (<i>Rhynchotaenia</i>) <i>nigricans</i>	102(2.43)	138(3.94)	13(1.63)	880(36.67)
<i>M.</i> (<i>Mansonina</i>) <i>pseudotitillans</i>	10(0.24)	2(0.06)		
<i>M.</i> (<i>Mansonina</i>) <i>titillans</i>	172(4.10)	43(1.23)	4(0.50)	118(4.92)
<i>M.</i> sp.	9(0.21)	1(0.03)		
<i>Psorophora</i> (<i>Janthinosoma</i>) <i>albipes</i>	43(1.02)	54(1.54)		35(1.46)
<i>P.</i> (<i>Grabhamia</i>) <i>cingulata</i>	14(0.33)	1(0.03)	4(0.50)	2(0.08)
<i>P.</i> (<i>Grabhamia</i>) <i>confinnis</i>	2(0.05)			
<i>P.</i> (<i>Janthinosoma</i>) <i>ferox</i>		3(0.09)		1(0.04)
<i>Limatus</i> <i>asulleptus</i>				
<i>Trichoprosopon</i> <i>digitatum</i>				
<i>T.</i> <i>longipes</i>				
<i>Wyeomia</i> sp.				
Psychodidae				
Phlebotominae				
	207(4.93)	547(15.63)		547(22.79)
Tabanidae				
<i>Chrysops</i> <i>varians</i>				
<i>C.</i> <i>varigatus</i>				
<i>Lepiselaga</i> <i>crassipes</i>				
<i>Tabanus</i> sp. 1		2(0.06)		1(0.04)
<i>T.</i> sp. 3				
TOTAL	4539(108.07)	4247(121.34)	165(20.63)	2224(92.67)

Table II-92. Hematophagous Diptera collected while alighting on
or biting man in forested areas on four ranches

Family/species	Barro			Buenos Aires			California			Cujada		
	Σ(No./Coll.)	Σ(No./Coll.)	Σ(No./Coll.)	Σ(No./Coll.)	Σ(No./Coll.)	Σ(No./Coll.)	Σ(No./Coll.)	Σ(No./Coll.)	Σ(No./Coll.)	Σ(No./Coll.)	Σ(No./Coll.)	Σ(No./Coll.)
Culicidae												
Anophelinae												
A. (Anopheles) pseudopunctipennis		1(0.02)									1(0.05)	
A. (Nyssorhynchus) albitarsis												
A. (Nyssorhynchus) darlingi												
A. (Nyssorhynchus) oswaldoi												
A. (Nyssorhynchus) triannulatus		2(0.05)									9(0.43)	
Culicinae												
A. (Ochlerotatus) crinifer		650(15.12)		243(7.36)		18(2.25)		189(9.00)				
A. (Ochlerotatus) scapularis		527(12.26)		535(16.21)		139(17.38)		67(3.19)				
A. (Ochlerotatus) serratus		367(8.53)		87(2.64)		63(7.88)		370(17.62)				
A. (Ochlerotatus) sp.		126(2.93)		280(8.48)		10(1.25)		59(2.81)				
Culex sp. lt. br.		5(0.12)		4(0.12)								
C. (Melanoconion) sp. dark		6(0.14)										
C. (Melanoconion) sp. black with spots				1(0.03)								
C. (Melanoconion) sp. golden spot		1(0.02)										
C. (Melanoconion) sp. tan												
Mansonia (Mansonia) humeralis											1(0.05)	
M. (Rhynchoetaenia) nigricans		46(1.07)		178(5.39)				245(11.67)				
M. (Mansonia) titillans		111(2.58)		25(0.76)		1(0.13)		102(4.86)				
M. sp.		5(0.12)										
Psorophora (Janthinosoma) albipes		625(14.53)		837(25.36)		185(23.13)		683(32.52)				
P. (Grabhamia) cingulata		35(0.81)		1(0.03)				2(0.10)				
P. (Grabhamia) confinnis												
P. (Janthinosoma) ferox		237(5.51)		63(1.91)		37(4.63)		63(3.00)				
Limatus asulleptus												
Trichoprosopon digitatum												
T. longipes		6(0.14)										
Wyeomia sp.		4(0.09)										
		10(0.23)		16(0.48)		1(0.13)		12(0.57)				
Tabanidae												
Chrysops varians												
C. varigatus		1(0.02)		4(0.12)		4(0.50)						
Lepiselaga crassipes		5(0.12)		2(0.06)		3(0.38)						
Tabanus sp. 1		2(0.05)		8(0.24)				1(0.05)				
T. sp. 2		1(0.02)		1(0.03)								
T. sp. 3		2(0.05)										
TOTAL												
		2775(64.53)		2285(69.24)		461(57.63)		1804(85.90)				

Table II-93 (cont)

<u>Family/species</u>	<u>Barro</u> <u>Σ(No./Coll.)</u>	<u>Buenos Aires</u> <u>Σ(No./Coll.)</u>	<u>Cuba</u> <u>Σ(No./Coll.)</u>
<u>Mansonia (Mansonia) humeralis</u>	56(0.64)	4(0.13)	10(0.31)
<u>M. (Rhynchotaenia) juxtamansonia</u>	45(0.51)	1(0.03)	
<u>M. (Rhynchotaenia) nigricans</u>	429(4.86)	49(1.53)	517(16.16)
<u>M. (Mansonia) pseudotitillans</u>	2(0.02)	1(0.03)	
<u>M. (Mansonia) titillans</u>	889(10.10)	70(2.19)	161(5.03)
<u>M. sp.</u>	9(0.10)		11(0.34)
<u>Psorophora (Janthinosoma) albipes</u>	99(1.13)	13(0.41)	8(0.25)
<u>P. (Grabhamia) cingulata</u>	39(0.44)	6(0.19)	15(0.47)
<u>P. (Grabhamia) confinnis</u>	9(0.10)	7(0.22)	12(0.38)
<u>P. (Janthinosoma) ferox</u>	6(0.07)	1(0.03)	
<u>Limatus asulleptus</u>			
<u>Trichoprosopon digitatum</u>			
<u>T. longipes</u>	10(0.11)	1(0.03)	
<u>Wyeomia sp.</u>			
Psychodidae			
Phlebotominae			
	1363(15.49)	41(1.28)	20(0.63)
Tabanidae			
<u>Chrysops varians</u>			
<u>C. varigatus</u>	1(0.01)	1(0.03)	
<u>Lepiselaga crassipes</u>	2(0.02)		
<u>Tabanus sp. 1</u>	2(0.02)	6(0.19)	
<u>T. sp. 3</u>	1(0.01)		
TOTAL	11,528(262.00)	744(23.25)	1706(53.31)

Table II-93. Hematophagous Diptera collected by light traps

placed in brushy areas at three ranches

Family/species	Barro	Buenos Aires	Cuba
	Σ (No./Coll.)	Σ (No./Coll.)	Σ (No./Coll.)
Ceratopogonidae	88(2.00)	80(2.50)	
Culicidae			
Anophelinae			
<u>Anopheles (Anopheles) neomaculipalpus</u>	6(0.07)		19(0.59)
<u>A. (Anopheles) pseudopunctipennis</u>		2(0.06)	2(0.06)
<u>A. (Anopheles) punctimacula</u>	6(0.07)	1(0.03)	3(0.09)
<u>A. (Lophodomyia) squamifemur</u>			
<u>A. (Nyssorhynchus) albitarsis</u>		6(0.19)	4(0.13)
<u>A. (Nyssorhynchus) albimanus</u>	2(0.02)		10(0.31)
<u>A. (Nyssorhynchus) darlingi</u>	5(0.06)	2(0.06)	1(0.03)
<u>A. (Nyssorhynchus) oswaldoi</u>	102(1.16)	8(0.25)	3(0.09)
<u>A. (Nyssorhynchus) triannulatus</u>			136(4.25)
<u>A. (Nyssorhynchus) sp.</u>	6(0.07)	6(0.19)	1(0.03)
Culicinae			
<u>Aedeomyia squamipennis</u>	1737(19.74)	52(1.63)	329(10.28)
<u>A. (Ochlerotatus) crinifer</u>	37(0.42)	4(0.13)	16(0.50)
<u>A. (Ochlerotatus) scupularis</u>	11(0.13)	3(0.09)	10(0.31)
<u>A. (Ochlerotatus) serratus</u>	15(0.17)	1(0.03)	
<u>A. (Ochlerotatus) sp.</u>	37(0.42)	1(0.03)	10(0.31)
<u>Culex sp. T. br.</u>	1185(13.47)	136(4.25)	139(4.34)
<u>C. sp.</u>	28(0.32)	2(0.06)	
<u>C. (Melanoconion) sp. br.</u>	137(1.56)	6(0.19)	16(0.50)
<u>C. (Melanoconion) sp. dark</u>	4786(54.39)	203(6.34)	164(5.13)
<u>C. (Melanoconion) sp. black</u>	128(1.45)	18(0.56)	1(0.03)
<u>C. (Melanoconion) sp. green pleura</u>	33(0.38)		3(0.09)
<u>C. (Melanoconion) black with spots</u>	184(2.09)	5(0.16)	4(0.13)
<u>C. (Melanoconion) sp. white tarsi</u>	6(0.07)	1(0.03)	2(0.06)
<u>C. (Melanoconion) sp. gold spot</u>	1(0.01)		48(1.50)
<u>C. (Melanoconion) sp. tan</u>	26(0.30)	3(0.09)	30(0.94)
<u>C. (Melanoconion) sp.</u>		3(0.09)	1(0.03)

Table II-94. Hematophagous Diptera collected while alighting on or biting man in brushy areas on three ranches

Family/species	Barro Σ(No./Coll.)	Buenos Aires Σ(No./Coll.)	Cuba Σ(No./Coll.)
Culicidae			
Anophelinae			
<u>A. (Anopheles) pseudopunctipennis</u>			
<u>A. (Nyssorhynchus) albitarsis</u>			
<u>A. (Nyssorhynchus) darlingi</u>			
<u>A. (Nyssorhynchus) oswaldoi</u>			
<u>A. (Nyssorhynchus) triannulatus</u>	1(0.03)		1(0.04)
Culicinae			
<u>A. (Ochlerotatus) crinifer</u>	442(13.00)	8(0.35)	193(8.39)
<u>A. (Ochlerotatus) scapularis</u>	230(6.76)	11(0.48)	30(1.30)
<u>A. (Ochlerotatus) serratus</u>	60(1.76)	3(0.13)	1(0.04)
<u>A. (Ochlerotatus) sp.</u>	16(0.47)		11(0.48)
<u>Culex sp. lt. br.</u>			
<u>C. (Melanoconion) sp. dark</u>			
<u>C. (Melanoconion) sp. black with spots</u>			
<u>C. (Melanoconion) sp. golden spot</u>			
<u>C. (Melanoconion) sp. tan</u>		1(0.04)	
<u>Mansonia (Mansonia) humeralis</u>			
<u>M. (Rhynchoetaenia) nigricans</u>	5(0.15)		5(0.22)
<u>M. (Mansonia) titillans</u>	75(2.21)		5(0.22)
<u>M. sp.</u>	1(0.03)		
<u>Psorophora (Janthinosoma) albipes</u>	1011(29.74)	51(2.22)	476(20.70)
<u>P. (Grabhamia) cingulata</u>	1(0.03)		25(1.09)
<u>P. (Grabhamia) confinnis</u>	3(0.09)		1(0.04)
<u>P. (Janthinosoma) ferox</u>	68(2.00)	1(0.04)	
<u>Limatus asulleptus</u>	1(0.03)		
<u>Trichoprosopon digitatum</u>	13(0.38)		
<u>T. longipes</u>	10(0.29)		1(0.04)
<u>Wyeomia sp.</u>	22(0.65)	1(0.04)	28(1.22)
Tabanidae			
<u>Chrysops varians</u>		5(0.22)	2(0.09)
<u>C. varigatus</u>	2(0.06)	4(0.17)	
<u>Lepiselaga crassipes</u>		1(0.04)	
<u>Tabanus sp. 1</u>		5(0.22)	
<u>T. sp. 2</u>		2(0.09)	
<u>T. sp. 3</u>			
TOTAL			
	1961(57.68)	93(4.04)	779(33.87)

Table II-95. Hematophagous Diptera collected in light traps at five sites in the Caucasus area

Family/species	Barro Σ(No./Coll.)	California Σ(No./Coll.)	Cuba Σ(No./Coll.)	Cujada Σ(No./Coll.)	Fisherman Σ(No./Coll.)
Ceratopogonidae					
	10(0.33)	46(1.31)		200(6.90)	
Culicidae					
Anophelinae					
<u>Anopheles (Anopheles) neomaculipalpus</u>	1(0.03)	9(0.26)	1(0.03)	4(0.14)	11(0.69)
<u>A. (Anopheles) pseudopunctipennis</u>			3(0.09)		
<u>A. (Anopheles) punctimacula</u>	2(0.07)	10(0.29)	13(0.37)	7(0.24)	
<u>A. (Lophodomyia) squamifemur</u>					
<u>A. (Anopheles) sp.</u>					
<u>A. (Nyssorhynchus) albitarsis</u>	2(0.07)	2(0.06)	1(0.03)	5(0.17)	3(0.19)
<u>A. (Nyssorhynchus) albimanus</u>					
<u>A. (Nyssorhynchus) darlingi</u>	2(0.07)	1(0.03)	2(0.06)	10(0.34)	1(0.06)
<u>A. (Nyssorhynchus) oswaldi</u>		2(0.06)		16(0.55)	
<u>A. (Nyssorhynchus) triannulatus</u>	9(0.03)	30(0.86)	23(0.94)	4194(144.62)	49(3.06)
<u>A. (Nyssorhynchus) sp.</u>	4(0.13)	4(0.11)		9(0.31)	
Culicinae					
<u>Aedeomyia squamipennis</u>	257(8.57)	22(0.63)	92(2.63)	434(14.97)	32(2.00)
<u>A. (Ochlerotatus) crinifer</u>	21(0.70)	12(0.34)	154(4.40)	4(0.14)	34(2.13)
<u>A. (Ochlerotatus) scupularis</u>	3(0.10)	6(0.17)	8(0.23)		7(0.44)
<u>A. (Ochlerotatus) serratus</u>		2(0.06)	3(0.09)		23(1.44)
<u>A. (Ochlerotatus) sp.</u>	7(0.23)	9(0.26)	149(4.26)	1(0.03)	22(1.38)
<u>Culex sp. T. br.</u>	61(2.03)	67(1.91)	103(2.94)	72(2.48)	2(0.13)
<u>C. sp.</u>	43(1.43)	5(0.14)			1(0.06)
<u>C. (Melanoconion) sp. br.</u>	17(0.57)	4(0.11)	18(0.51)	10(0.34)	44(2.75)
<u>C. (Melanoconion) sp. dark</u>	79(2.63)	60(1.71)	114(3.26)	106(3.66)	
<u>C. (Melanoconion) sp. black</u>	1(0.03)		26(0.74)	1(0.03)	
<u>C. (Melanoconion) sp. green pleura</u>	9(0.30)	5(0.14)	6(0.17)	3(0.10)	13(0.81)
<u>C. (Melanoconion) black with spots</u>	2(0.07)	2(0.06)	1(0.03)		
<u>C. (Melanoconion) sp. white tarsi</u>	2(0.07)		1(0.03)	1(0.03)	
<u>C. (Melanoconion) sp. gold spot</u>	2(0.07)	4(0.11)	4(0.11)	59(2.03)	
<u>C. (Melanoconion) sp. tan</u>	16(0.53)	4(0.11)	13(0.37)	274(9.45)	21(1.31)
<u>C. (Melanoconion) sp.</u>	2(0.07)		10(0.29)		

Table II-95 (cont)

<u>Family/species</u>	<u>Barro</u> <u>Σ(No./Coll.)</u>	<u>California</u> <u>Σ(No./Coll.)</u>	<u>Cuba</u> <u>Σ(No./Coll.)</u>	<u>Cujada</u> <u>Σ(No./Coll.)</u>	<u>Fisherman</u> <u>Σ(No./Coll.)</u>
<u>Mansonina (Mansonina) humeralis</u>	8(0.27)	2(0.06)	2(0.06)	272(9.38)	127(7.94)
<u>M. (Rhynchotaenia) juxtamansonina</u>					
<u>M. (Rhynchotaenia) nigricans</u>	21(0.70)	25(0.71)	63(1.80)	1263(43.55)	37(2.31)
<u>M. (Mansonina) pseudotitillans</u>					
<u>M. (Mansonina) titillans</u>	68(2.27)	72(2.06)	130(3.71)	901(31.07)	252(15.75)
<u>M. sp.</u>		1(0.03)		9(0.31)	10(0.63)
<u>Psorophora (Janthinosoma) albipes</u>			60(1.71)	22(0.76)	25(1.56)
<u>P. (Grabhamia) cingulata</u>	3(0.10)	94(2.69)	71(2.03)	3(0.10)	15(0.94)
<u>P. (Grabhamia) confinnis</u>	41(1.37)	74(2.11)	31(0.89)	2(0.07)	20(1.25)
<u>P. (Janthinosoma) ferox</u>	1(0.03)				
<u>Limatus asulleptus</u>					
<u>Trichoprosopon digitatum</u>					
<u>T. longipes</u>					
<u>Wyeomia sp.</u>					
Psychodidae					
Phlebotominae					
	39(1.30)	46(1.31)	27(0.77)	31(1.07)	12(0.75)
Tabanidae					
<u>Chrysops varians</u>					
<u>C. varigatus</u>				1(0.03)	
<u>Lepiselaga crassipes</u>				6(0.21)	
<u>Tabanus sp. 1</u>		3(0.09)		1(0.03)	
<u>T. sp. 3</u>					
TOTAL	733(24.43)	623(17.80)	1129(32.26)	7921(273.14)	761(47.56)

Table II-96 Hematophagous Diptera collected while alighting on or biting man at five sites in the Caucasus area

Family/species	Barro Σ (No./Coll.)	California Σ (No./Coll.)	Cuba Σ (No./Coll.)	Cujada Σ (No./Coll.)
Culicidae				
Anophelinae				
<u>A. (Anopheles) pseudopunctipennis</u>				1(0.05)
<u>A. (Nyssorhynchus) albitarsis</u>	1(0.04)			
<u>A. (Nyssorhynchus) darlingi</u>	1(0.04)			
<u>A. (Nyssorhynchus) oswaldoi</u>	1(0.04)	1(0.04)		
<u>A. (Nyssorhynchus) triannulatus</u>			3(0.11)	
Culicinae				
<u>A. (Ochlerotatus) crinifer</u>	771(27.54)	36(1.57)	2262(80.79)	4(0.19)
<u>A. (Ochlerotatus) scapularis</u>	81(2.89)	181(7.87)	294(10.50)	
<u>A. (Ochlerotatus) serratus</u>	42(1.50)		60(2.14)	
<u>A. (Ochlerotatus) sp.</u>	104(3.71)		439(15.68)	
<u>Culex sp. lt. br.</u>		6(0.26)		
<u>C. (Melanoconion) sp. dark</u>				
<u>C. (Melanoconion) sp. black with spots</u>				
<u>C. (Melanoconion) sp. golden spot</u>				
<u>C. (Melanoconion) sp. tan</u>				
<u>Mansonina (Mansonina) humeralis</u>				1(0.05)
<u>M. (Rhynchotaenia) nigricans</u>	2(0.07)			2(0.10)
<u>M. (Mansonina) titillans</u>	1(0.04)	1(0.04)	15(0.54)	2(0.10)
<u>M. sp.</u>	12(0.43)		10(0.36)	25(1.19)
<u>Psorophora (Janthinosoma) albipes</u>				
<u>P. (Grabhamia) cingulata</u>	290(10.36)	110(4.78)	432(15.43)	23(1.10)
<u>P. (Grabhamia) confinnis</u>	4(0.14)	10(0.43)	18(0.64)	
<u>P. (Janthinosoma) ferox</u>	9(0.32)	4(0.17)	20(0.71)	
Limnatiidae				
<u>Limatus asulleptus</u>				
<u>Trichoprosopon digitatum</u>				
<u>T. longipes</u>				
<u>Wyeomia sp.</u>			20(0.71)	2(0.10)
Tabanidae				
<u>Chrysops varians</u>				
<u>C. varigatus</u>			2(0.07)	
<u>Lepiselaga crassipes</u>				
<u>Tabanus sp. 1</u>				
<u>T. sp. 2</u>				
<u>T. sp. 3</u>				
TOTAL	1319(47.11)	349(15.17)	3575(127.68)	60(2.86)

Phlebotomine sand flies collected in the Caucasia region*

Lutzomyia camposi (Rodriguez) 1952

L. carpenteri (Fchld. and Hertig) 1953

L. cayennensis cayennensis (Floch and Abonnenc) 1941

L. gomezi (Nitz) 1931

L. nordestina (Mang.) 1942

L. olmeca-bicolor Fchld. and Theodor 1971

L. panamensis (Shannon) 1926

L. shannoni (Dyar) 1929

L. trapedoi (Fchld. and Hertig) 1953

L. trinidadensis (Newstead) 1922

L. triramula (Fchld. and Hertig) 1953

L. yuilli Young and Porter 1972

*Determinations made by David G. Young, Department of Entomology, University of Florida

Table II-98

Tabanidae collected in the Caucasia region

Chrysops varians Wiedemann 1828 var. *tardus* Wiedemann 1828

Chrysops variegatus (DeGeer) 1776

Chrysops variegatus (DeGeer) 1776 var. *venezuelensis* Krober 1925

Diachlorus curvipes (Fabricius) 1805

Dichelacera (*Dichelacera*) *scapularis* Macquart 1847 var. *aquilus* Fairchild

Leucotabanus exaestuans (Linnaeus) 1758

Lepiselaga crassipes (Fabricius) 1805

Tabanus claripennis (Bigot) 1892

Tabanus lutzi Krober 1934

Tabanus nebulosus DeGeer 1776

Tabanus olivaceiventris Macquart 1847

Tabanus pungens Wiedemann 1828

Tabanus dorsiger Wiedmann 1821 var. *dorsovittatus* Macquart 1855

Table II-98

Preliminary list of the species of Culex occurring in the Caucasia region

Culex (Melanoconion)

aikenii	(Aiken), 1906
sp. close to	albinensis, Bonne-Wepster and Bonne, 1919(1920)
bastagarius	Dyar and Knab, 1906
chrysonotum	Dyar and Knab, 1908
conspirator	Dyar and Knab, 1906
dunni	Dyar, 1918
educator	Dyar and Knab, 1906
egcymon	Dyar, 1923
elephas	Komp, 1936
elevator	Dyar and Knab, 1906
epanastasis	Dyar, 1922
intrincatus?	Brethes, 1916
oedipus	Root, 1927
serratimarge	Root, 1927
taeniopus	Dyar and Knab, 1907
tecmaris	Dyar, 1918
thomasi?	Evans, 1924

C. (Mochlostyrax)

hesitator	Dyar and Knab, 1907
-----------	---------------------

C. (Eubonnea)

amazonensis	(Lutz), 1905
-------------	--------------

C. (Culex)

corniger group	
declarator	Dyar and Knab, 1906
mollis	Dyar and Knab, 1906
nigripalpus	Theobald, 1901
usquatissimus,	Dyar, 1922
usquatus?	Dyar, 1918

Acknowledgements

The generosity of Dr. Raúl Londoño in sharing his ranch, our base for field operations, is acknowledged. The late Mr. Lutz Bayer made the entomological reconnaissance of the area and selected many of the study sites. Charles Porter assisted with the identification of insects of the area. Norman Peterson and Fabio Nelson Zuluaga (with the aid of the administration of the Veterinary Faculty, Universidad de Antioquia) provided logistical support.